

HISTORICAL ECOLOGY: A NEW APPROACH TO STUDYING THE EVOLUTION OF ECOLOGICAL ASSOCIATIONS

DANIEL R. BROOKS¹

ABSTRACT

Historical ecology is presented as a complementary approach to evolutionary ecology. The prime distinction between the two approaches is the use of direct estimates of history in explanations by the former and of indirect estimates of history by the latter. Direct estimates of history are obtained by using phylogenetic systematics. They require analysis of many species simultaneously. Indirect estimates can be applied in individual cases and include such concepts as: (1) equating number of species in an ecological association with the age of the association; (2) equating the geographic range of a species with its age; and (3) equating the specificity of ecological interactions with the length of time species have been associated. Historical ecological methods have been applied in three general areas: (1) the historical context of geographic distribution patterns; (2) the historical context of ecological associations; and (3) the historical context of particular ecological life history traits. A unified quantitative approach allows historical ecological analysis for individual clades or aggregates of clades. Among the most interesting general conclusions that are forthcoming from the historical ecological perspective are those that differ from the evolutionary ecological view. These include: (1) ecological diversification lags behind morphological diversification historically; (2) degree of specificity is not a thoroughly reliable indicator of the age of an association; (3) resource tracking models of coevolution seem to include unacceptable assumptions; and (4) maximum competition scenarios are indistinguishable from random association scenarios. Future studies promise to be fruitful.

A number of fundamental and general questions have held the attention of ecologists for over a century. Why are species distributed in the manner they are? Why are certain species associated with each other ecologically, and how long have such associations existed? And, why do certain species have the ecological life history traits they do, and under what circumstances did those traits emerge? In the past 125 years, biology has operated under an evolutionary paradigm, a stance that I think has been undeniably productive. The search for causal mechanisms responsible for observed attributes has concentrated on evolutionary, that is historical, mechanisms. In ecology, this has led to the emergence of the field called evolutionary ecology.

In presenting what I will call historical ecology as a newly-emerging field, I do not wish to ignore the contributions of previous workers who were interested in problems of history and ecology. From the standpoint of parasitology, at least, my views simply represent the most recent refinement of a tradition extending back over 90 years.

Von Ihering (1891, 1902) was impressed by faunal similarities between southern South America and Australasia and faunal differences between northern and southern South America. In the first study, von Ihering used data con-

cerning the distributions of temnocephalid turbellarians and their crustacean hosts to postulate an ancient freshwater connection between South America and Australasia. He reasoned that if similar appearing hosts were inhabited by the same or closely-related parasites they were themselves closely related and not products of convergent evolution. In the latter study, von Ihering considered parasitic helminths in assessing the origins and evolution of South American mammals. He concluded the following: (1) North and South America were not connected in their present configuration until the Pliocene, (2) South American mammals include an autochthonous element, that originated and evolved in South America, and a heterochthonous element that invaded South America from the north subsequent to the Pliocene, (3) helminths of the autochthonous mammals are highly endemic whereas the helminths inhabiting the heterochthonous mammals include many occurring in other, Holarctic, mammals. Von Ihering asserted that data on host-parasite relationships in general constituted a "... valuable aid in analytical study of zoogeography and paleogeography."

Kellogg (1896) suggested that avian biting lice gave evidence of the genetic (= phylogenetic) relationships between their hosts. "The occurrence

¹ Department of Zoology, University of British Columbia, 2075 Westbrook Mall, Vancouver, British Columbia V6T 2A9, Canada.

of a parasitic species common to European and American birds, which is not an infrequent matter, must have another explanation than any yet suggested. This explanation I believe is, for many of the instances, that the parasitic species has persisted unchanged from the common ancestor of the two or more now distinct but closely-allied bird-species" (Kellogg, 1896: 51). As examples, Kellogg (1913) listed shared mallophagan species in American and European avocets, coots and bitterns, American and Old World water-ousels and kinglets, and New World and Old World crows. Kellogg and Kuwana (1902) found that 19 of 44 (43%) mallophagan species collected from Galapagos birds also occurred on Central and North American birds.

An Australian student of avian mallophaga, Harrison (1911, 1914, 1915a, 1915b, 1916, 1922) considered host-parasite data significant for phylogeny reconstruction, using the same rationale as Kellogg. "Owing to both environment and food remaining unchanged through the centuries, these insects have not differentiated as fast as their hosts, and afford indications of original relationship between birds that have diverged widely from parent stock" (Harrison, 1911). Following the above-cited papers which concerned elucidations of avian phylogenetic relationships using parasite data, Harrison began using parasite data to support the notion of ancient Australia-Antarctic-South American land connections (Harrison, 1924, 1926, 1928a, 1928b, 1929). Harrison's work influenced some conclusions published by Johnston (1912, 1914, 1916) concerning phylogenetic relationships of hosts inhabited by the same or closely-related parasite species.

Metcalf, an American protozoologist, published a number of papers (e.g., 1920, 1922, 1923a, 1923b) in which he examined the paleogeographical and phylogenetic implications of opalinid ciliates and their anuran hosts. In 1929, Metcalf published a summary account of the ideas of von Ihering, Kellogg, Harrison, and himself, and concluded that all four had arrived at the same conclusions independently but that no one had added to the approach advocated by von Ihering. Therefore, he suggested that the appellation, "the von Ihering Method," was appropriate for studies of the historical relationships among hosts, parasites, and geography.

The above authors used a method based on occurrences of the same parasite in similar hosts in disjunct geographical regions. Fahrenholz

(1913) discussed the phylogenetic significance of host-parasite relationships without regard for geographical distributions and without any assumption that hosts speciate while parasites do not. Fahrenholz (1913: 371) stated (author's translation): "From studies of parasitic mites in 1907, the question occurred to me: Is it possible to make definitive conclusions about their [hosts] phylogeny from the occurrence of the same or related parasites in different hosts? This statement should be answered in the affirmative. Because parasites are dependent, as living creatures, on their surrounding living conditions, so in general should the same type of parasite occur in the same type of host and with hosts of differing form the parasites should deviate from one another to the same degree as their hosts are related by kinship [verwandt sein]."

Hennig (1966) suggested that Fahrenholz considered host-parasite relationships a matter of general habitat preference and not phylogenetic phenomena. For example: "Obviously blood-sucking parasites—here the lice—must have particular dependence on the blood of the host so that the true lice (Anoplura) in varying hosts deviate from one another to a degree in the way the blood of the latter is different. Consequently, the lice would clearly mirror the blood relationships (Blutverwandschaft) of the respective host animals to a certain degree" (Fahrenholz, 1913: 372). Although the use of *verwandten* is ambiguous, I believe that Fahrenholz considered host-parasite information valid data relating to host phylogenies: "Thus one conclusion: on the grounds of the lice brought forward for discussion—in agreement with the blood studies—the catarrhine monkeys (Menschenaffen) stand much nearer to humans than to the remaining apes" (Fahrenholz, 1913: 374).

Thus, between 1891 and 1923 at least five workers arrived independently at similar conclusions, namely that host-parasite relationships were a manifestation of a phenomenon pertinent to phylogeny or historical changes. Subsequently, a number of authors attempted to explain parasite relationships in terms of hosts and formulated general "rules" about the evolution (= phylogenesis) of hosts and parasites (Andrews, 1927; Baer, 1948; Cameron, 1964; Darling, 1921; Dogiel, 1964; Dougherty, 1949; Eichler, 1941a, 1941b, 1948; Ewing, 1924, 1926; Hegner, 1928; Hopkins, 1942; Kirby, 1937; Manter, 1940, 1954, 1955, 1963, 1966; Metcalf, 1940; Pritchard, 1966; Stammer, 1957; Szidat,

1956, 1960; Zschokke, 1933). The rules form a small group of interrelated concepts:

1. Fahrenholz's Rule (see Eichler, 1941a, 1941b; Stammer, 1957; Cameron, 1964; Dogiel, 1964; Hennig, 1966; Ashlock, 1974): *Parasite phylogeny mirrors host phylogeny.*

2. Szidat's Rule (see Szidat, 1956, 1960): *The more primitive the host, the more primitive the parasites it harbors.*

3. Manter's Rules (see Manter, 1955, 1966; Inglis, 1971): (1) *Parasites evolve more slowly than their hosts;* (2) *the longer the association with a host-group, the more pronounced the specificity exhibited by the parasite group;* (3) *a host species harbors the largest number of parasite species in the area where it has resided longest, so if the same or two closely-related species of host exhibit a disjunct distribution and possess similar faunas, the areas in which the hosts occur must have been contiguous at a past time.*

4. Eichler's Rule (see Eichler, 1941a, 1941b, 1948; Inglis, 1971): *The more genera of parasites a host harbors, the larger the systematic group to which the host belongs.*

Two concepts of ecological associations appeared independently and nearly simultaneously, in systematics (von Ihering, 1891 and others discussed above) and in ecology (e.g., Verschaffelt, 1910; Brues, 1920). Almost immediately, specialists in each field found themselves in disagreement with each other regarding their understanding of the causes and manifestations of such associations (e.g., Dunn, 1925). This was due, in my opinion, to differences in interests or motivations coupled with a similar methodological approach. To a great extent, systematists were trying to record what had occurred between host group and parasite group during the course of phylogenesis. This was accomplished by describing as many associations as possible in terms of the hypothesis that members of the association exhibited congruent phylogenies. Often, the notion that such congruent phylogenesis was also related to changing geography was also included. Ecologists, however, were intent upon trying to determine if there was any historical (i.e., phylogenetic) significance to the interactions they observed. Most recent discussions have followed Ehrlich and Raven (1964), who asserted that such studies provide little data concerning phylogenies: "Although the data we have gathered permit us to make reasonable sequence predictions about phylogenetic patterns . . . , these predic-

tions cannot be tested and the relationships cannot be specified further in the absence of a fossil record. The reconstruction of phylogenies on the basis of this sort of information would seem an unwarranted imposition on the data, since evolutionary rates and time are inseparable." Other ecologists had felt somewhat differently. Brues (1920: 315) wrote: "As we might *naturally* [emphasis mine] expect, it is possible to point out in a very general way a progressive specialization in the selection of food-plants which parallels to some degree what appears to have been the path of evolution among insects, as determined by the criteria furnished by comparative anatomy, development, and paleontology."

Between 1940 and 1966, the connection between systematics and ecology certainly became attenuated. The former assumed a progressively more passive role in evolutionary biology, summarizing the findings of the latter. There is a noticeable lack during this period, at least in parasitology, of direct comparisons between host and parasite phylogenies, and a steadily increasing reliance on degree of host specificity as the best indicator of historical association. In my opinion this was due to two different aspects of the emergence of neo-Darwinism as the prevailing evolutionary theory. The most obvious aspect is that neo-Darwinism is a theory of ecological determinism; various ecological factors operating on random variation produce historically contingent evolutionary change. Under such a paradigm the determination of close ecological interactions is much more important than matching phylogenies, whose congruence or lack thereof has little consequence for the theory. It is also possible that matching phylogenies seemed too much like directed evolution to many neo-Darwinists. Indeed, Kellogg wrote about the demise of Darwinism at the turn of the century and Metcalf was a leading spokesman for the American orthogenesis movement (Bowler, 1983). For whatever combination of reasons, attempts at explicit assessment of the historical components of ecological associations played a minor role during a period of more than 25 years.

Manter (1966) attempted to generalize host-parasite relationships further by describing parasites as a subset of the total characters of a given host species available for use in phylogenetic analysis. Hennig (1966) expressed similar views but considered symbiont data a form of "chorological" data to be fitted a posteriori to the host-group cladogram. He further stressed com-

parisons of parasite data and geographic distribution data (chorological data *sensu strictu*). Manter (1966) stated: "Parasites . . . furnish information about present-day habits and ecology of their . . . hosts. These same parasites also hold promise of telling us something about host and geographical connections of long ago. They are simultaneously the product of an immediate environment and of a long ancestry reflecting associations of millions of years. The messages they carry are thus always bilingual and usually garbled."

In 1972, H. H. Ross published two papers (1972a, 1972b) that dealt with explicit assessment of the historical context of ecological diversity in communities, especially of insects. Ross asked: "What are the ecological shifts which have occurred during phylogenesis?" "How do they arise?" and "How often do they arise?" By ecological shifts, Ross meant geographic and host changes, as well as changes in ecological life history traits. I consider these studies to comprise the seminal papers in the field which I will call *historical ecology*.

It will be my thesis in this review that evolutionary ecology as a field attempts to answer historical questions by using indirect estimates of history. This is not meant to be a criticism of evolutionary ecology. Rather, it is meant to provide a distinction that hopefully will make it possible to show that there is a place for a complementary approach. I will refer to this complementary approach as historical ecology, distinguished by virtue of its dependence on direct estimates of history in formulating evolutionary explanations for ecological associations.

I will begin by stating what I consider to be indirect and direct estimates of history. By indirect estimates, I mean such as the following: (1) equating the number of species in an ecosystem with the age of the system; (2) equating the geographic range of a species with its age; and (3) equating the specificity of ecological interactions with the age of the association denoted by the set of interacting species (see e.g., Boucot, 1983a). Direct estimates of historical aspects of ecology are achieved by the use of phylogenetic systematic methods. In the most recent past, a number of workers have suggested that use of phylogenetic systematic techniques could help investigations in historical ecology (Hennig, 1966; Michener, 1967; Ross, 1972a, 1972b; Ashlock, 1974). Thus, the distinction between the two approaches is not between qualitative and quan-

titative measures, because both approaches have quantified protocols. The rest of this review will explicate three general types of questions that can be addressed by historical ecology and will consider the extent to which such efforts do in fact constitute an approach complementing evolutionary ecology. The examples that I will present are drawn from my research on the helminth parasite faunas of lower vertebrates, but I hope to show that the principles involved can be extended to any type of ecological association.

I. How did species occurring in a given area come to be in that area?

This question encompasses two topics, the means by which a particular distribution was achieved and how long ago it took place. An historical answer can be provided for individual species or for entire community assemblages. I will provide examples of each.

One of the fundamental advances of the past 20 years in evolutionary biology has been the formal articulation of two different perspectives on the general manner by which species achieve their geographical distributions. These perspectives may be categorized loosely as the "island biogeography" paradigm (MacArthur & Wilson, 1967) and the "vicariance biogeography" paradigm (Croizat et al., 1974; Platnick & Nelson, 1978; Rosen, 1975, 1985). The first paradigm calls attention to the propensity for organisms to move about and the second reminds us that those movements may not be unconstrained. Among those most responsible for documenting the extent to which geographic distributions are not random assemblages were Cain (1944), Camp (1947), and Wulff (1950). In general, the perspective offered by both views is this: a species may be represented in a particular area because it evolved elsewhere and dispersed into that area, or it may occur in the area because it evolved there. In the first instance, the dispersal may have occurred a long time ago or relatively recently; in either case, there is no reason to expect the species' history to be coordinate with the history of the area into which it dispersed. In the second instance, the species' history must be coordinate with the history of the area.

It is at this point that an empirical distinction between evolutionary ecology and historical ecology can be seen. Evolutionary ecology may be limited to indirect measures of history but

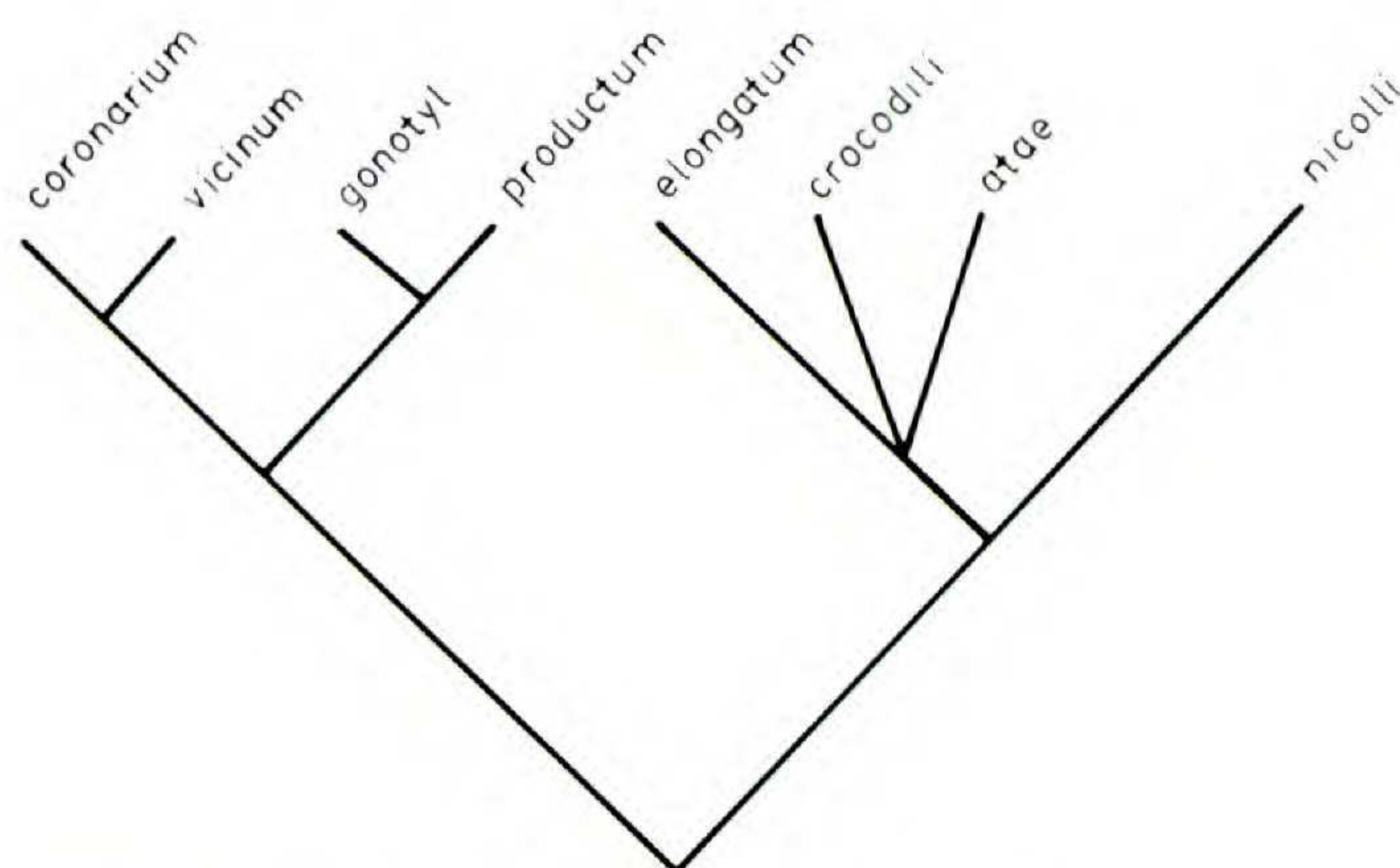


FIGURE 1. Cladogram depicting phylogenetic relationships of *Proctocaecum* species (redrawn from Brooks, 1981a).

these can be applied to a single species or a single ecological association. Historical ecology by contrast, can provide direct estimates of history, but only if a number of close relatives for each species represented in any given association are considered. Let us consider the following example.

The genus *Proctocaecum* comprises a monophyletic group of digenetic trematodes inhabiting the intestines of crocodilians. Figure 1 depicts a phylogenetic tree for *Proctocaecum* (see Brooks, 1981a). The relationships suggested by the phylogenetic tree can be superimposed on a map (Fig. 2) and the question of vicariance or dispersal can be asked. We note in Figure 2 that some of the contemporary species of *Proctocaecum* are separated from each other by ocean that

crocodilians today do not traverse. In the case of these parasites, we also know that specific gastropod molluscs and some sort of small fish are required for completion of the life cycle; the dispersal abilities of any parasite are constrained by the least vagile of its hosts. If we look at past geographic configurations to find the most recent period in which dispersal of this group of parasites could be accomplished (Fig. 3), we notice that the sequence of speciation events suggested by the cladogram is coordinate with the geological history of the areas in which those species occur. This is highly suggestive that whatever dispersal might have occurred did not have an impact on the differentiation of species, which occurred in a manner coordinate with the history of the areas in which they now occur. In this example, our suspicion of vicariance, i.e., history, as the explanation for the geographic distribution of members of *Proctocaecum* is strengthened by observation that other digenetic trematodes inhabiting crocodilians exhibit the same distribution patterns (Fig. 4; see also Brooks, 1979a).

It is highly likely that many, if not most, ecological associations contain both vicariant and dispersalist elements. It is important to assess which components of an ecological association belong in each category in order to provide some assessment of the context in which particular interactions or ecological life history traits emerged. Historically associated lineages will all corre-

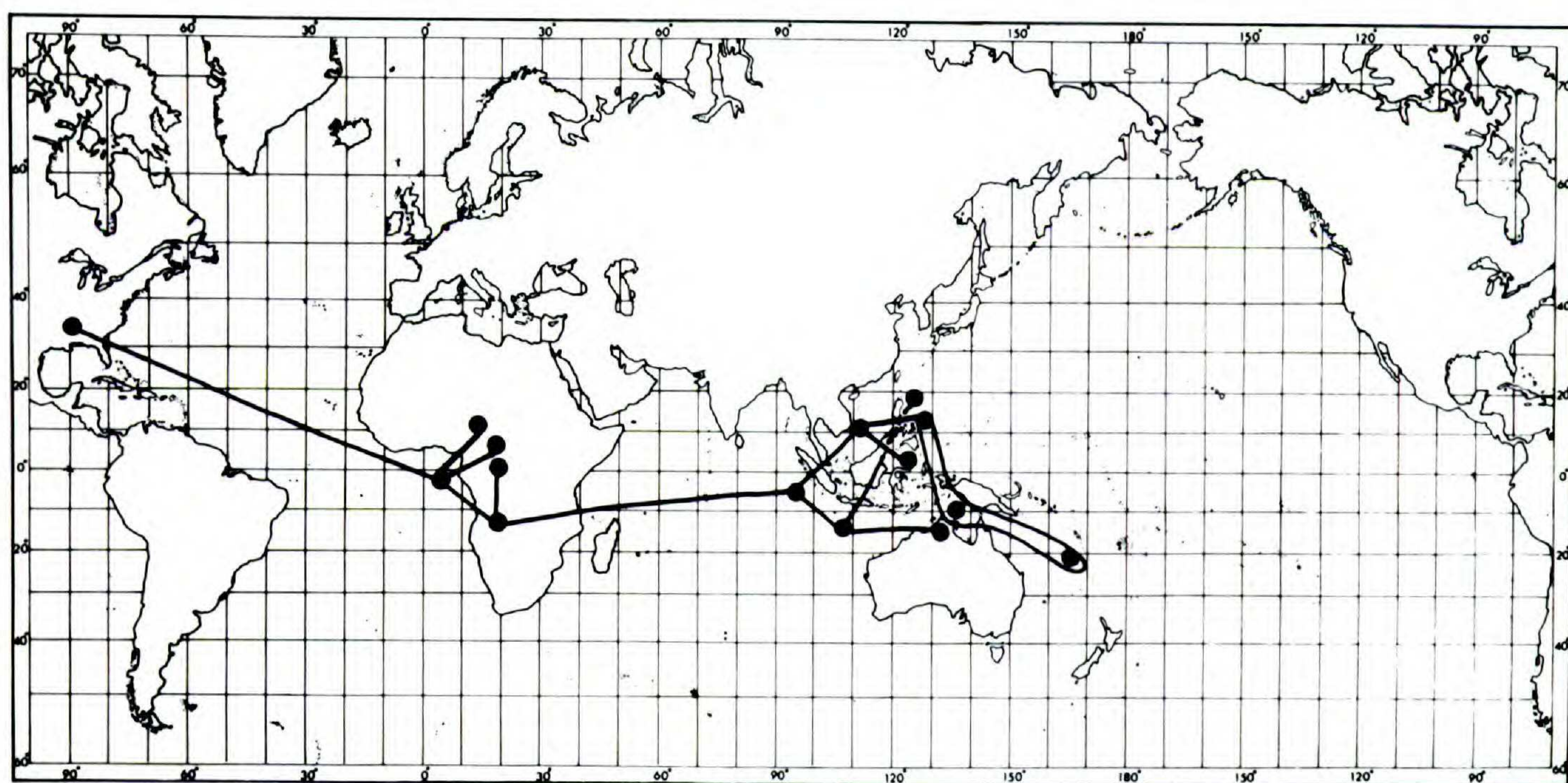


FIGURE 2. Cladogram depicting phylogenetic relationships of *Proctocaecum* species superimposed on map depicting contemporary geography (redrawn from Brooks, 1979a).

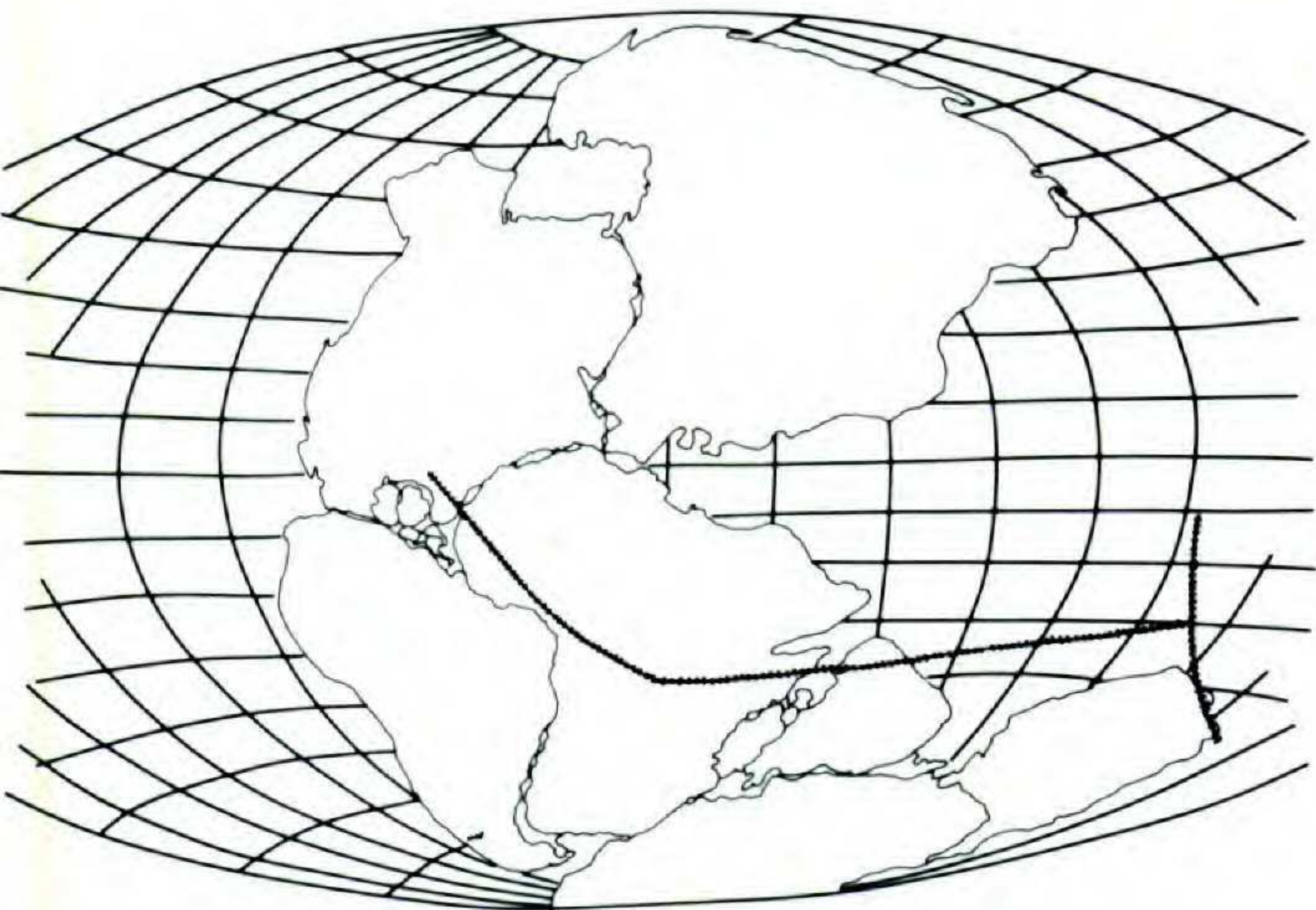


FIGURE 3. Distribution pattern indicated by phylogenetic relationships of *Proctocaecum* species overlaid on map depicting geography of the time period during which the study taxon could have achieved its present distribution (redrawn from Brooks, 1979a).

spond to the same set of interrelationships of the areas in which their component species now occur. Species that differentiated in other areas will support different patterns or relationships of areas. Any historically determined core of a given ecological association will be characterized by a set of species whose lineages have coordinate histories. Thus, it is not necessary to compare each lineage with geographic history, as one would if one were simply interested in historical biogeographic questions (cf. Rosen, 1985). Multi-lineage comparisons can be performed qualitatively (Platnick & Nelson, 1978; Nelson & Platnick, 1981; Rosen, 1985), or quantitatively.

The quantitative protocol has been presented by Brooks (1981b) and will be discussed in the next section as well. It is based on the notion

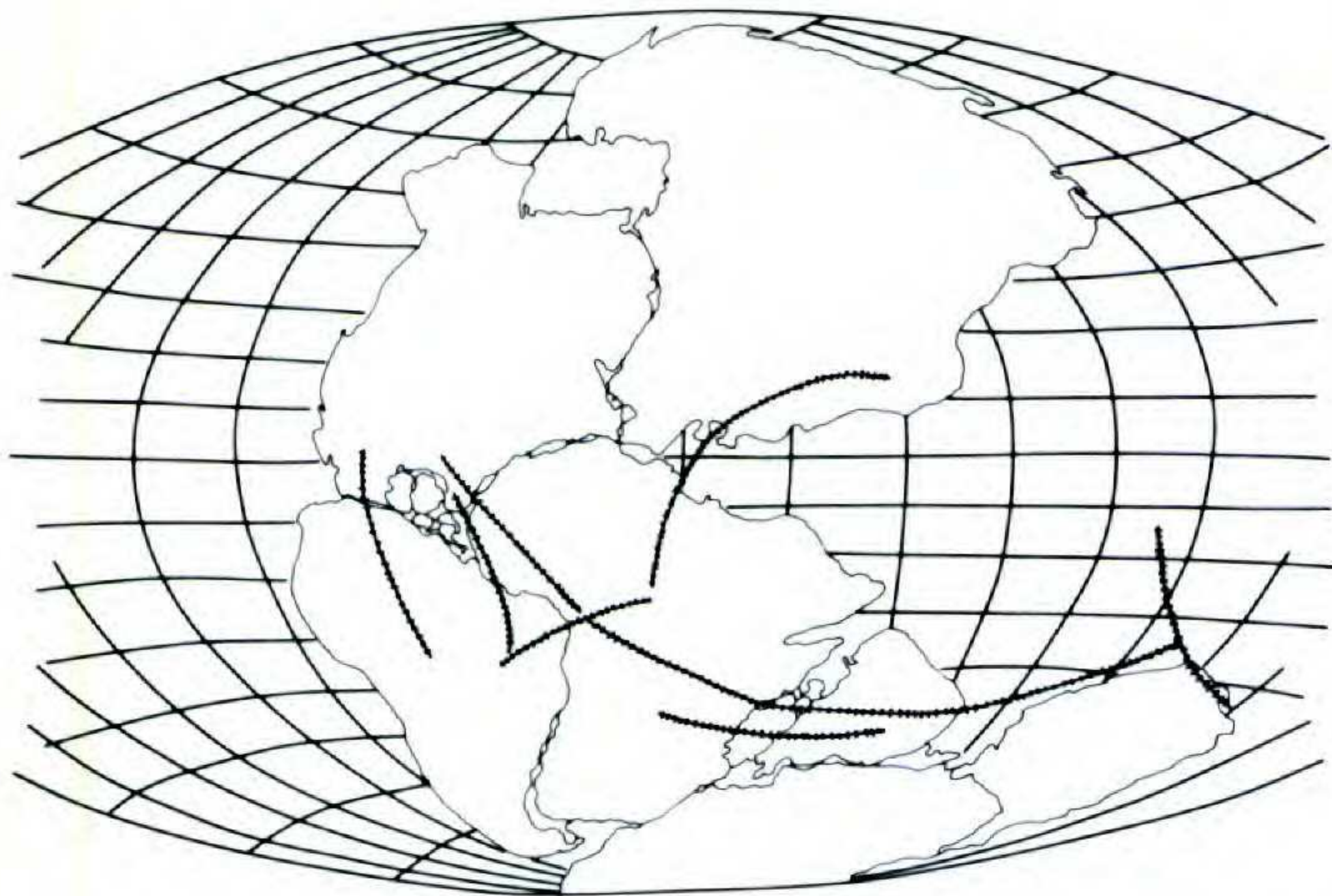


FIGURE 4. Generalized distribution patterns indicated by phylogenetic relationships of various groups of digenetic trematodes inhabiting crocodilians (redrawn from Brooks, 1979a).

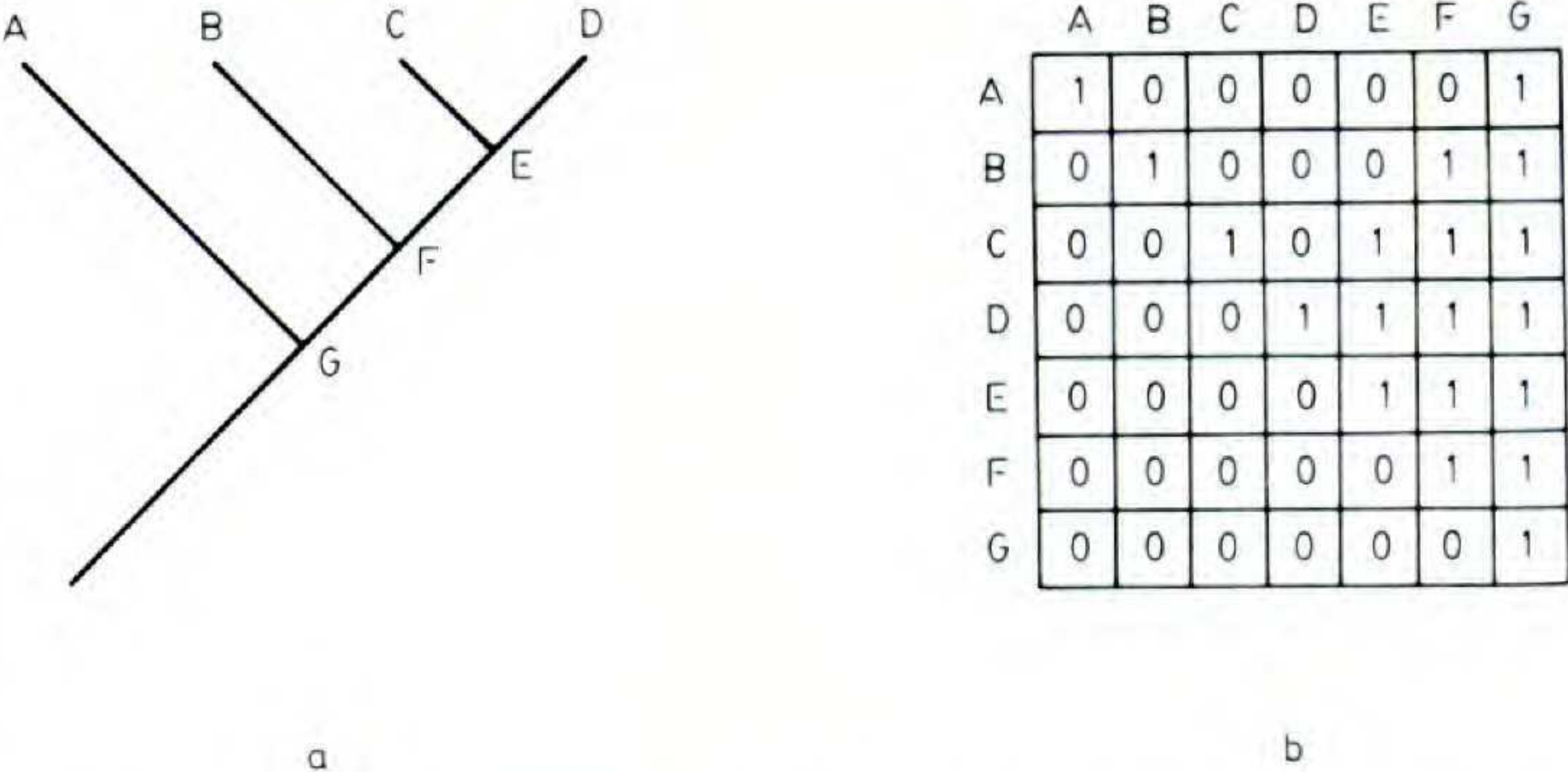


FIGURE 5. Conversion of a cladogram (a) into a matrix of binary variables (b).

that species can be considered characters of the areas in which they occur, and that lineages of species can be considered transformation series linking different areas in a historical pattern. Any given phylogenetic tree (Fig. 5a) can be converted into a matrix of binary characters (Fig. 5b) which can then be analyzed phylogenetically to indicate the pattern of relationships between the evolution of the clade and the areas in which the various known species occur. Any number of groups can be analyzed together using this technique, producing a summary statement of the historical context of the species composition in the ecological associations considered.

As an application of the above protocol, I have considered the parasitic helminths inhabiting neotropical freshwater stingrays and the areas in which they are known to occur [for a summary of the taxa, their phylogenetic relationships and their geographic distributions, see Brooks et al.

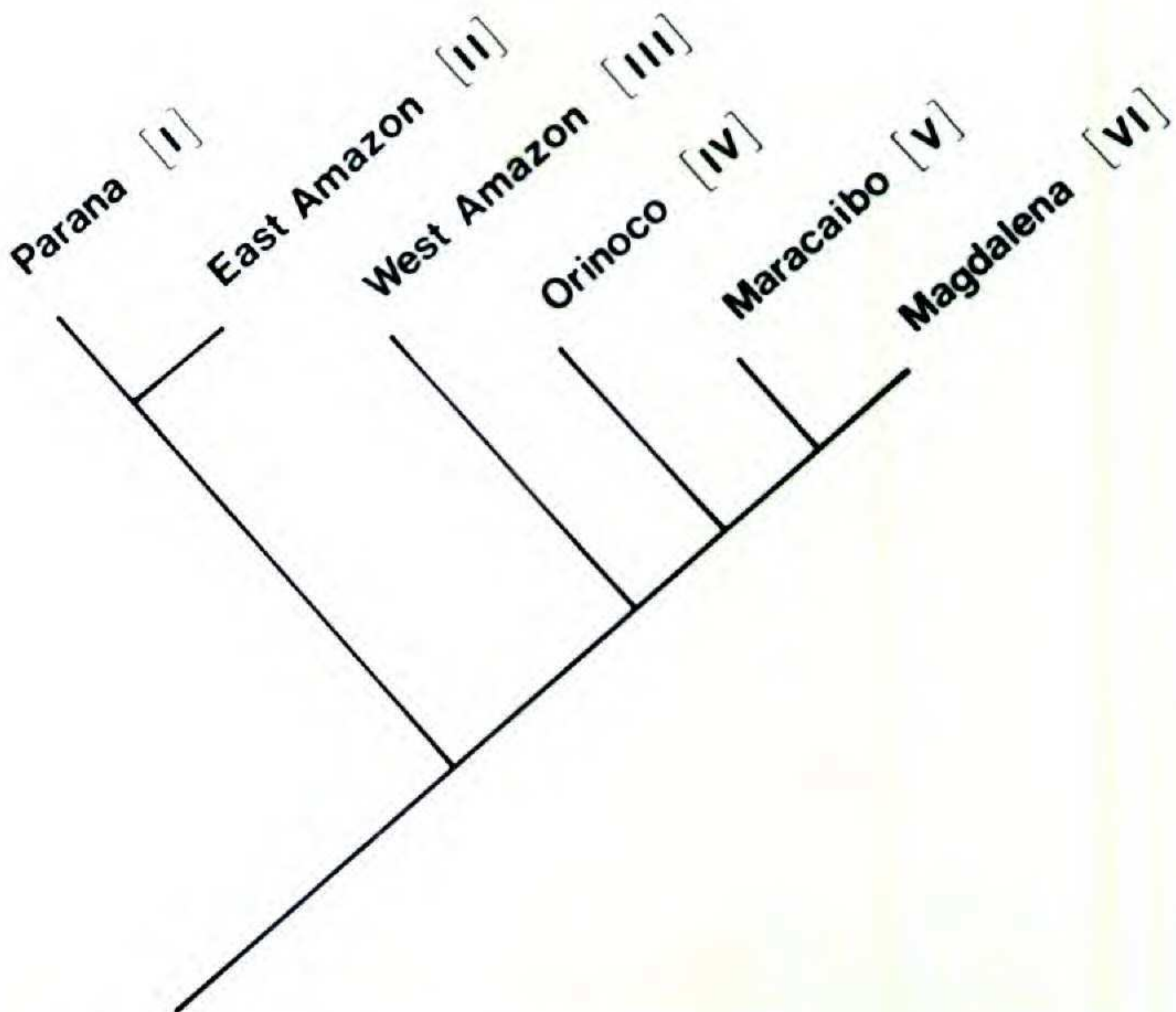


FIGURE 6. Summary cladogram depicting relationships among six areas (I–VI) in South America, based on phylogenetic relationships of helminth parasites inhabiting freshwater stingrays and living in those areas.

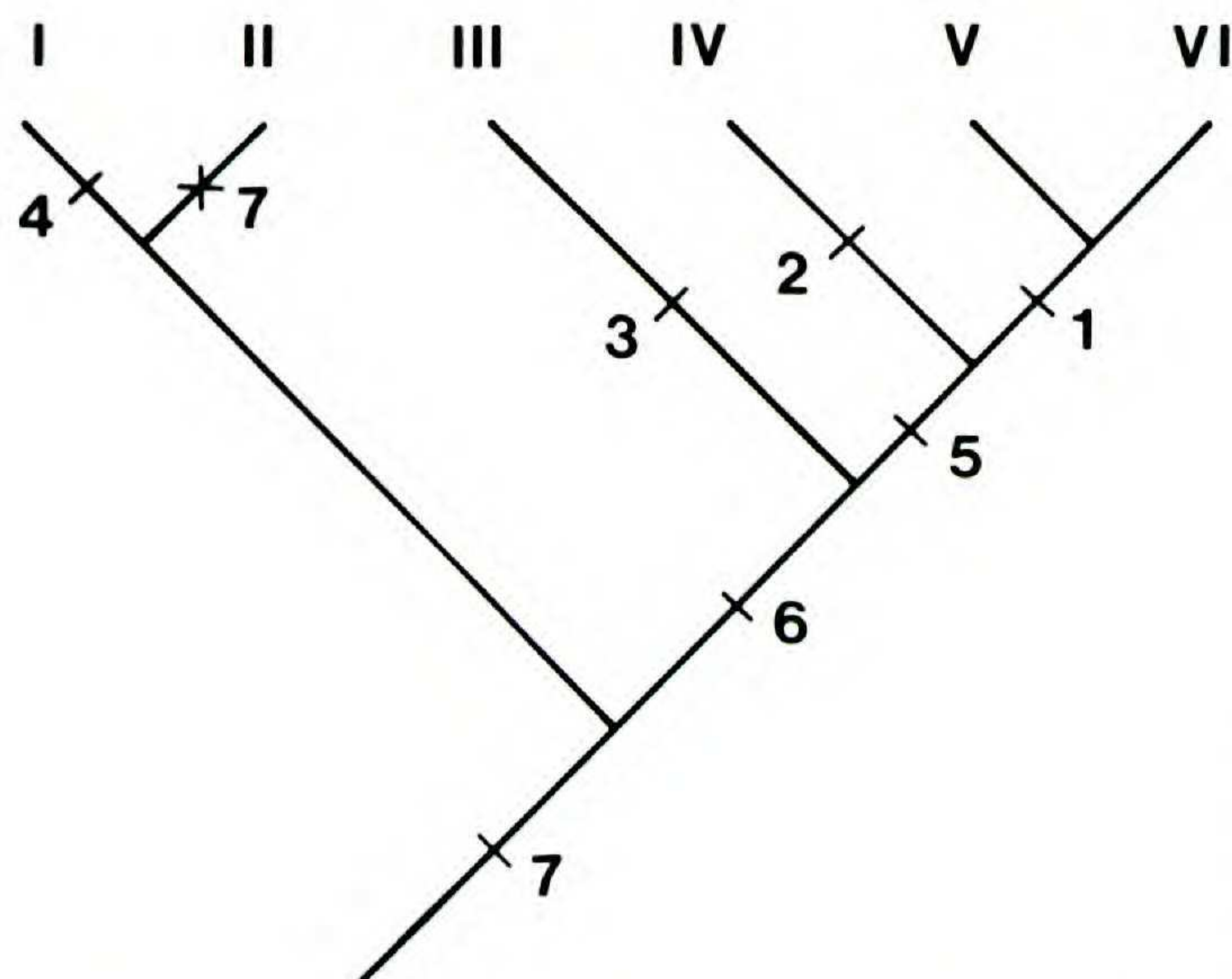


FIGURE 7. Summary cladogram from Figure 6 with numerical codes for genus *Acanthobothrium* indicated. 1 = *A. quinonesi*; 2 = *A. regoi*; 3 = *A. amazonensis*; 4 = *A. terezae*; 5 = common ancestor of 1 and 2; 6 = common ancestor of 3 and 5; 7 = common ancestor of 4 and 6. Slash marks accompanying numbers indicate presence in taxa; x mark indicates absence in area of predicted presence based on historical hypothesis.

(1981a), Brooks et al. (1981b) and Brooks (1981b)]. Figure 6 represents the relationships among six geographic areas based on the phylogenetic relationships of the parasites. Figure 7 shows the distribution of traits for a wholly vicariant group, the members of the genus *Acanthobothrium*. Each species (Nos. 1–4) and its inferred ancestor (Nos. 5–7) occurs only once on the cladogram, indicating perfect fit of the phylogenetic tree to the set of relationships among the areas. The only possible discrepancy (signified by 7X on area II) indicates a lack of any records for *Acanthobothrium* in area II (East Amazon). Based on the fit of the rest of the areas and *Acanthobothrium*, we would expect to find either *A. terezae* (4) or an undescribed species most closely related to *A. terezae* in area II. The distribution of members of *Potamotrygonocetus* (Fig. 8a), however, indicates a large amount of dispersal. Such dispersal can be inferred in two ways. First, there are four instances of observations (2 of 10X, one each of 11X and 12X) incongruent with the area relationships. Second, the phylogenetic tree for *Potamotrygonocetus* that best fits the observed distribution, shown in Figure 8b, suggests that taxon 10 is the ancestor of taxon 11. Phylogenetic analysis of the morphology of *Potamotrygonocetus* species places taxon 10 (*P. amazonensis*) as the sister-species of taxon 11, not its ancestor. Thus, this second

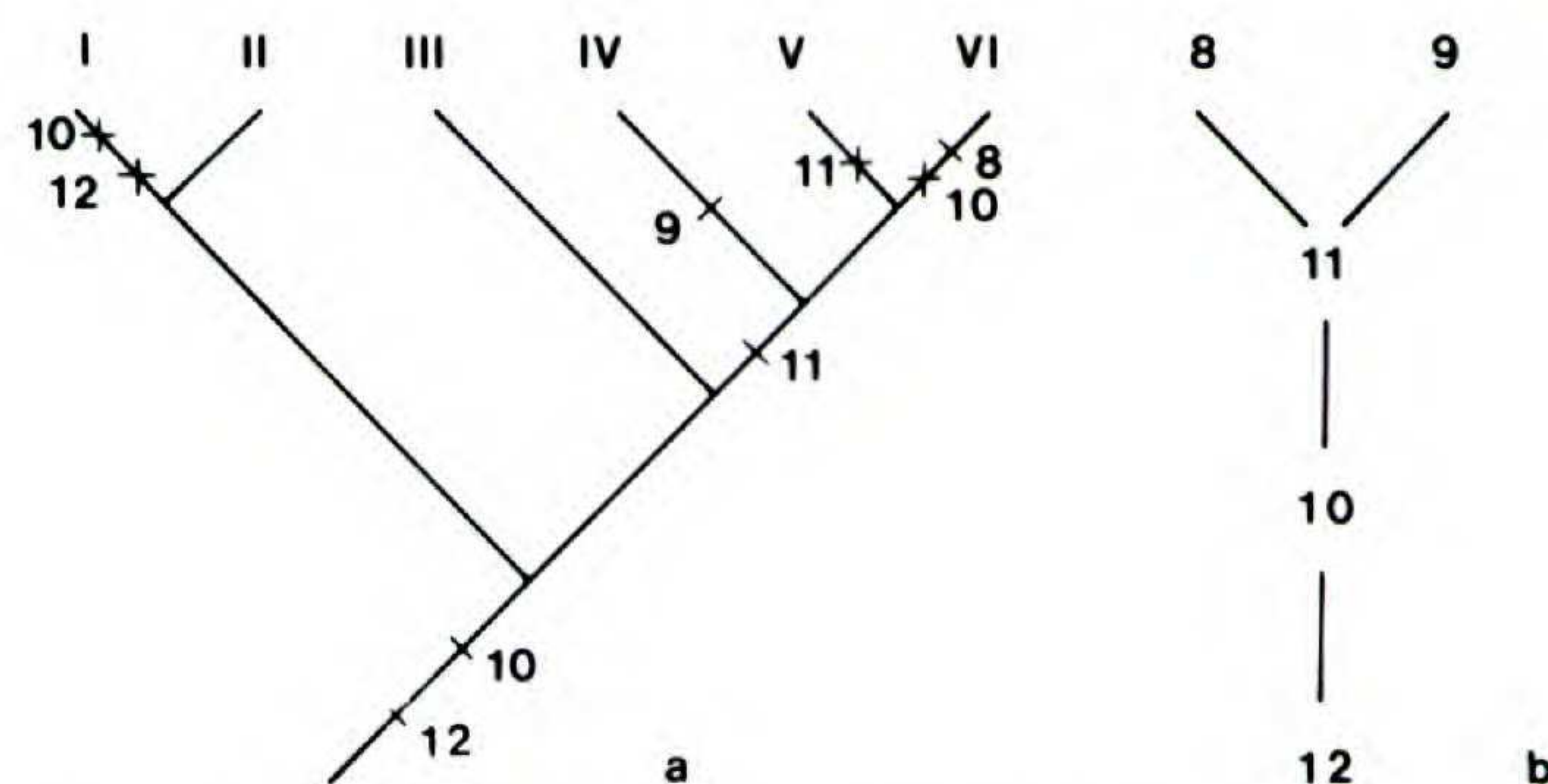


FIGURE 8. Summary cladogram from Figure 6 with numerical codes for genus *Potamotrygonocetus* indicated (a) and most parsimonious arrangement of numerical codes based on observed distributions (b). 8 = *P. magdalenensis*; 9 = *P. orinocoensis*; 10 = *P. amazonensis*; 11 = common ancestor of 8 and 9; 12 = common ancestor of 10 and 11.

view of the summary cladogram provides evidence of another historical incongruence between *Potamotrygonocetus* spp. and the areas in which they occur. This is due, apparently, mostly to widespread dispersal of *P. amazonensis*.

In the case of *Acanthobothrium*, of the 8 notations on the summary cladogram, 7 are congruent with its phylogeny, yielding a consistency index (Kluge & Farris, 1969) of 87.5%, whereas for *Potamotrygonocetus* the consistency index is only 4 out of 9 or 44.4%.

Below are summary statements about the evolution of the six communities.

Parana. There is no indication of colonization of Parana rays by parasites differentiated in other areas. Nor do we know of any local parasites that have expanded their habitats to include potamotrygonids. Of the six communities identified, this appears to be the earliest one differentiated (see Brooks et al., 1981b). Subsequently, there appears to have been a good deal of dispersal from the Parana to the East Amazon to the Orinoco following differentiation of the Parana fauna, but little dispersal into it.

West Amazon. This area also shows no indication of colonization of rays from other areas, or from local parasites normally associated with non-stingray hosts. It contains two species that are widespread in distribution. The Parana community is its closest, and apparently vicariant, relative.

Magdalena. With the exception of one species that also occurs in the Maracibo area, all known parasites found in stingrays in this area are endemics. This includes *Paravitellotrema over-*

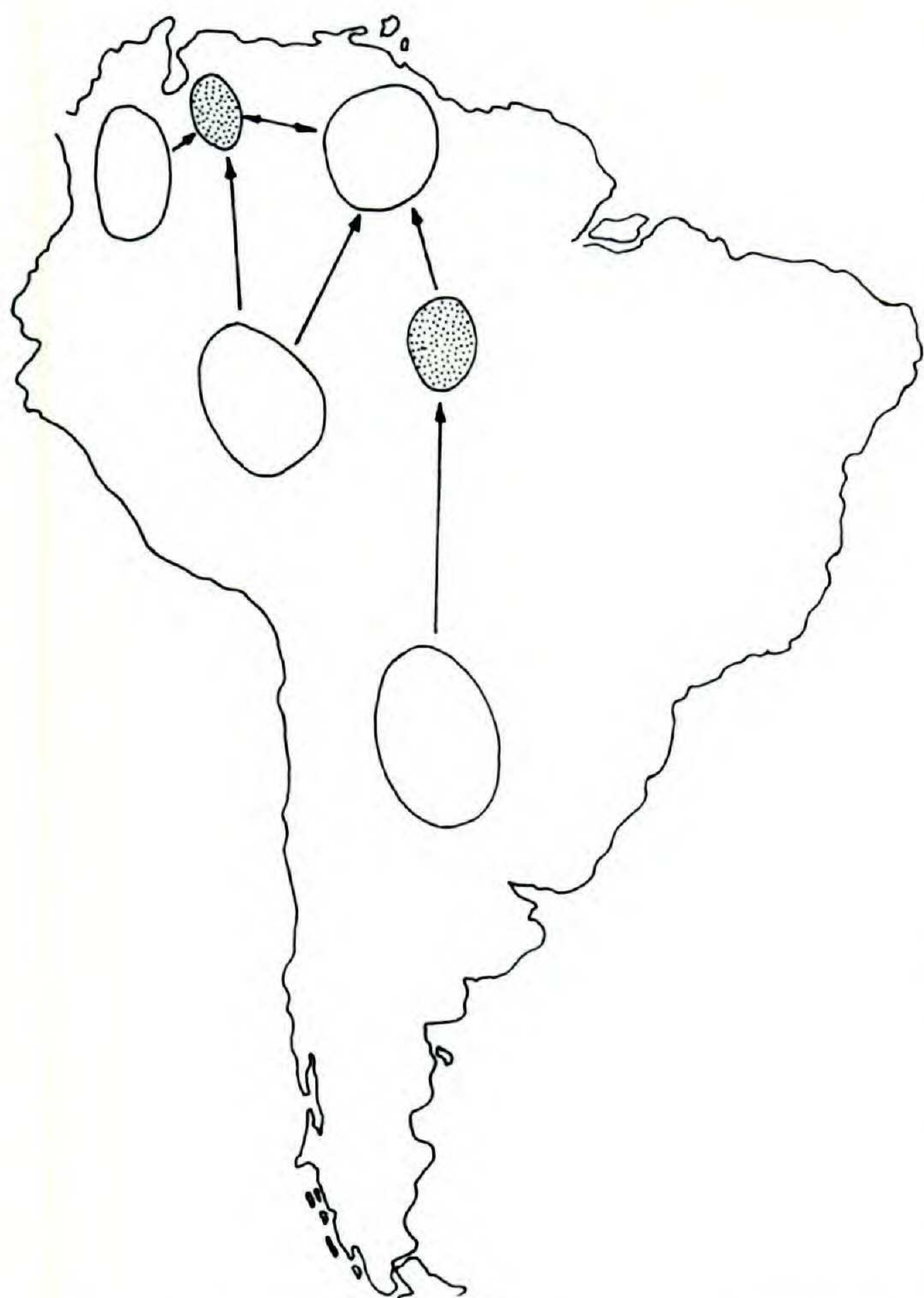


FIGURE 9. Summary of sources of community members for six communities of freshwater stingray parasites in South America. The four encircled areas represent communities having a substantial historical/coevolved core. The two areas indicated by shaded triangles are communities having at most a single endemic species. The arrows indicate non-historical contributions from one community to another. Refer to text for particulars.

streeti, which represents a group of digeneans normally parasitizing siluriform and characid teleosts. The other endemics apparently vicariated in the area, with one species dispersing into the Maracaibo area.

The above three communities appear to be primarily vicariant communities some of whose members have dispersed into other areas. The next three communities present more interesting histories.

Maracaibo. This area has only a single, endemic, species of stingray. That stingray is known to host three species of helminth parasites, *Acanthobothrium quinonesi* from the Magdalena fauna, *Potamotrygonocetus amazonensis* from the West Amazon fauna, and *Rhinebothroides venezuelensis* from the Orinoco fauna. With apparent colonizing influences from three different communities, each with endemic species of *Acanthobothrium*, *Potamotrygonocetus*, and

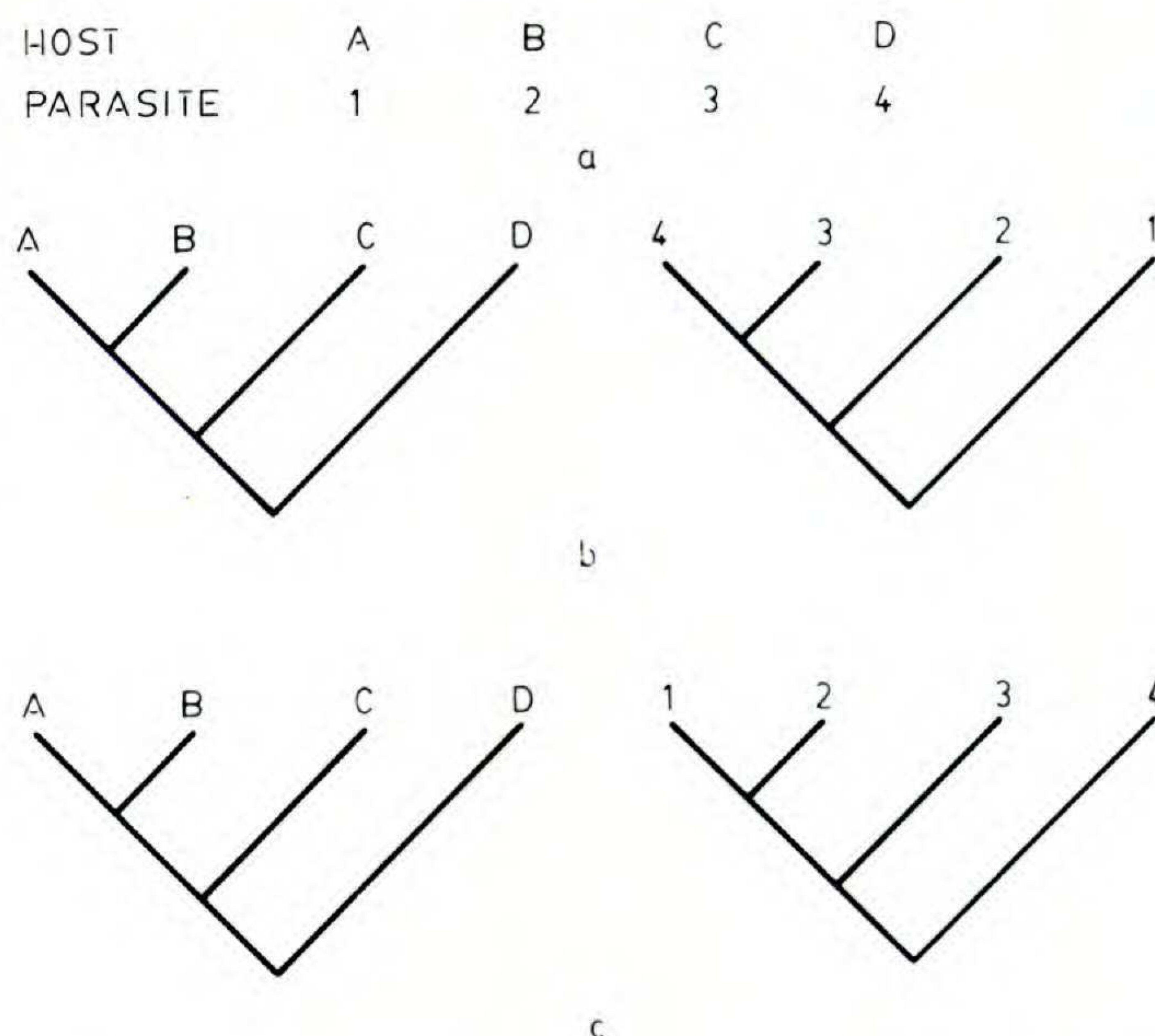
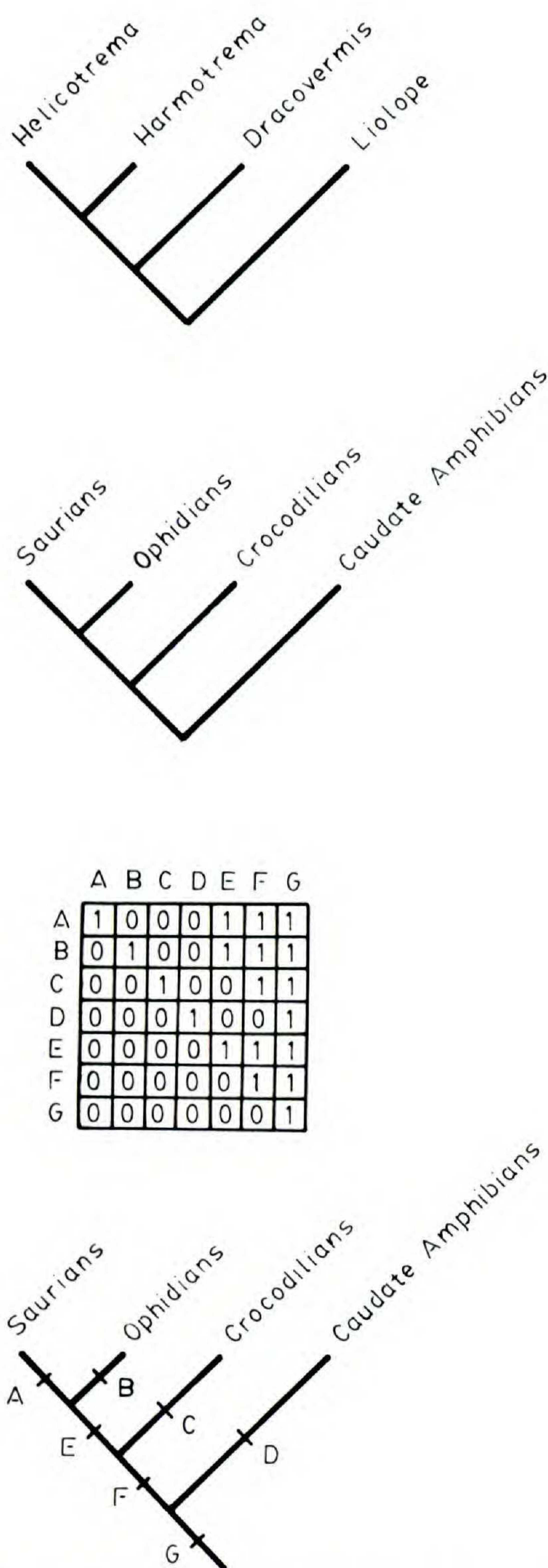


FIGURE 10. Observed associations between pairs of species (a), resulting from historical association (b), or from colonization (c) (redrawn from Brooks & Mitter, 1984).

Rhinebothroides, it is interesting that only a single species in each genus is established in the Maracaibo area. Perhaps this indicates something of the competitive abilities of the various parasites or perhaps it simply reflects uneven dispersal of suitable intermediate hosts. The latter seems more likely when Maracaibo is contrasted with the Orinoco (see below). The topology of the relationships among these parasites and their host does not differ from that in endemic areas.

East Amazon. There is only one endemic species of stingray helminth found in this area, *Rhinebothroides freitasi*. One other species is a colonizer from the West Amazon fauna. Several species have been acquired secondarily from local teleostean hosts. The rest are derived from the Parana fauna through dispersal. This community comes closest to being an "island biogeography" assemblage.

Orinoco. This area contains two different major faunas of potamotrygonid parasites, one derived through vicariance and one derived through dispersal from the Parana through the East Amazon with subsequent differentiation. To the first group belongs *Rhinebothroides venezuelensis*, *Potamotrygonocetus orinocoensis*, *Acanthobothrium regoi*, and *Echinocephalus daileyi*. To the second belongs *Rhinebothrium paratrygoni*, *Eutetrarhynchus araya*, and *Rhinebothroides scorzai* and *R. glandularis*. In contrast with Maracaibo, where a restricted fauna comprising a single species from three different faunas occurs, two faunas coexist in the Orinoco. If we



FIGURES 11–14. Documenting degree of historical association between members of ecological associations.—11. Cladogram of four genera comprising the trematode family Liolopidae.—12. Cladogram representing phylogenetic relationships of hosts for liolopids.—13. Matrix of binary characters representing cladogram (a) in Figure 10.—14. Host relationships predicted by phylogenetic relationships of their liolopid parasites (redrawn from Brooks, 1981b).

include the occurrence of *Potamotrygonocetus amazonensis* from the West Amazon fauna via dispersal, and the occurrence of *Megapriapus ungriai* from local teleosts, more than two faunas coexist. That this coexistence is real may be at-

tested to by the fact that specimens of all three species of *Rhinebothroides* known from the Orinoco have been collected in a single host.

One difference between the Maracaibo and Orinoco faunas may be the occurrence of at least three species of potamotrygonid stingrays in the Orinoco and only one in Maracaibo. Brooks' (1981b) analysis of the host–parasite relationships of potamotrygonids using the analytical technique described herein placed two of those hosts, *Potamotrygon hystrix* and *P. reticulatus*, in different parts of the cladogram (see Fig. 15). *Potamotrygon reticulatus* was related more closely to the Parana rays examined (*P. falkneri*), and *P. hystrix* was more closely related to *P. circularis* from the West Amazon. The Orinoco thus acts like two or three communities that have joined to form a larger community. Figure 9 summarizes the sources of components in these various communities.

Evolutionary ecologists are interested in the effects of different kinds of ecological phenomena, such as colonization, competition, and sympatric speciation. Information of the sort provided by this kind of study could be used to identify effective ecological associations that owe their present configuration to different processes.

II. How do two or more species with a “close and evident ecological relationship” (sensu Ehrlich & Raven, 1964) come to be related that way?

This is the question addressed by the concept of coevolution as defined by Brooks (1979b), Mitter and Brooks (1983), and Brooks and Mitter (1984). Associated species (Fig. 10a) may be so because they inherited an ecological relationship from their ancestors; this is a state of *association by descent*. Alternatively, species may be associated presently but differentiated prior to their association; this is *association by colonization*. In the first case, the histories of the two associates will be coordinate (Fig. 10b) and, in the second, they will not be coordinate (e.g., Fig. 10c).

One type of ecological association for which such evidence is fairly abundant is that of host–parasite associations. For example, Figure 11 depicts the relative phylogenetic relationships of four groups of vertebrates, and Figure 12 is a cladogram of four genera of closely related digenetic trematodes. Following the method of Brooks (1981b), the parasite cladogram can be considered a character-state tree, or transfor-

mation-series (Hennig, 1966), of the host group, converted into a matrix of binary codes (Fig. 13), and used to classify the hosts (Fig. 14). Points of agreement between host phylogeny and parasite-derived host relationships support association by descent; points of disagreement represent episodes of colonization. Note the parallels between the documentation of historical and non-historical associations between species and the documentation of historical and non-historical geographic distributions.

This parallel can be extended to include analysis of more complex systems than two-species interactions. Consider a multi-species ecological association. Those having historical associations will all have coordinate histories, whereas colonizers will each have a unique connection with the association. Figure 15 presents two different groups that have slightly different speciation patterns but that both have historical associations with the same host group. Note that the host relationships postulated by both parasite groups are the same. For any parasite fauna, or for any multi-species ecological association, the pattern of host relationships supported by coordinate parasite phylogenies will be coordinate with the host phylogeny. From a summary cladogram produced in this manner (e.g., Fig. 16), summary statements about the historical components of an ecological association can be produced. The digenetic trematode fauna of crocodilians, for example, comprises many species acquired by colonization from predatory fish (through ingestion of common intermediate hosts). Despite this, analysis of the total fauna either qualitatively (Brooks, 1979a) or using the method discussed above (Brooks, 1981b) shows agreement with the host group phylogeny. Recently, a student in my laboratory (O'Grady, unpubl. data) has shown that the phylogenetic relationships of nematode parasites of crocodilians, which also include a number of colonizers, produce a summary statement of host relationships coordinate with host phylogeny.

Before moving on to the third area of discussion, I would like to mention an alternative quantitative approach. This is the "nearest neighbor" method of Mickevich (1981), introduced as a tool in analytical biogeography. In his study of crocodilian nematodes, O'Grady (unpubl. data) compared results obtained using both Brooks' (1981b) and Mickevich's (1981) methods. The results were the same in both cases. Thus, it appears that there is a unified quanti-

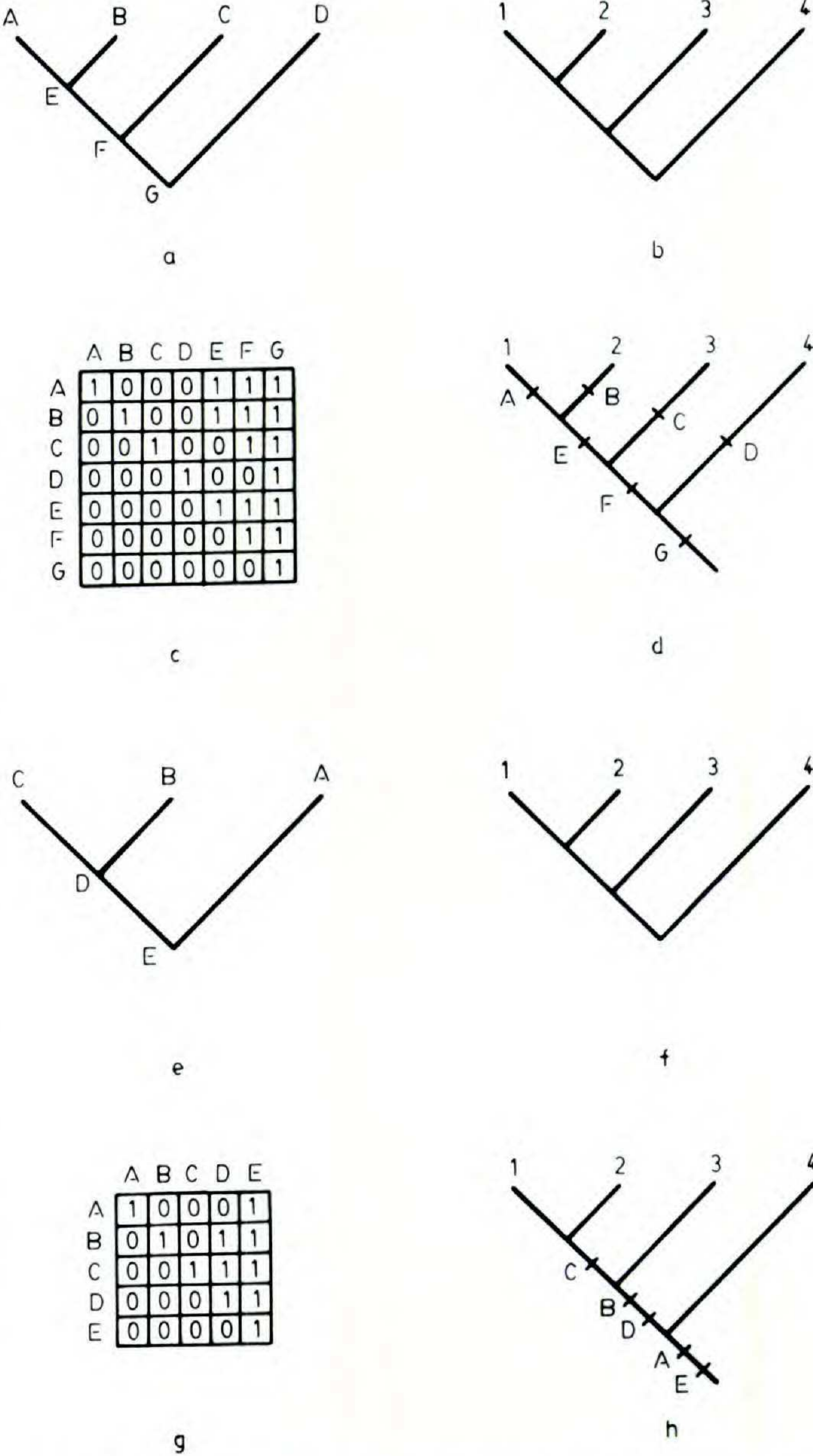


FIGURE 15. Finding congruent historical aspects of ecological associations. (a) and (e) are cladograms for groups of taxa associated with another group [(b) and (f)], (c) and (g) are binary matrices representing cladograms in (a) and (e), (d) is a cladogram depicting fit of phylogenetic relationships of the group in (a) to the group in (b), and (h) is a cladogram depicting fit of phylogenetic relationships of the group in (e) to the group in (f) (redrawn from Brooks, 1981b).

tative approach, at least implicitly, available for studies of historical ecology.

III. Under what conditions did the ecological life history traits that we observe today emerge?

This category provides historical ecological contributions to questions concerning the evolutionary effects of competition and the occurrence of adaptive radiations. It allows possible distinction between factors responsible for the maintenance of traits seen today and factors responsible for the emergence of those traits in the

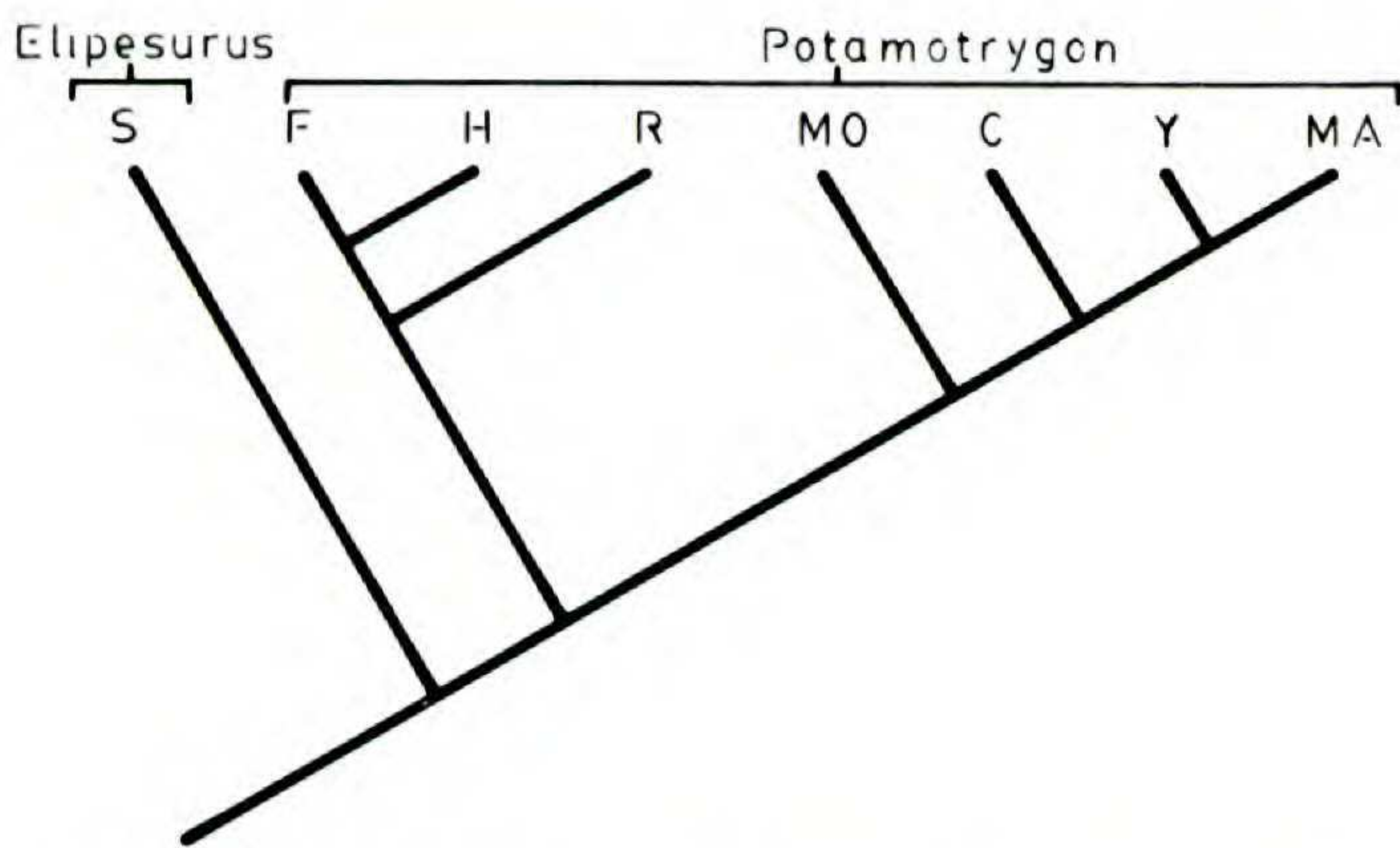


FIGURE 16. Cladogram depicting phylogenetic relationships among eight species of neotropical freshwater stingrays based on the phylogenetic relationships of their helminth parasites (redrawn from Brooks, 1981b).

first place (see also Ross, 1972b). Evolutionary ecology, by virtue of its reliance on indirect estimates of history, must rely on a form of uniformitarianism—if competition maintains traits today, it was responsible for their origin in the past.

Historical analysis also allows one to compare the relative degree of parallel (sometimes called adaptive) evolution exhibited by different groups. Parasites, for example, are supposed to be paradigms of adaptive radiations (Price, 1977, 1980). And yet, recent studies of various groups of parasitic worms (Brooks & Glen, 1982; Brooks et al., 1985a, 1985b) have documented consistency indices of 0.74 to 0.95, suggesting very low levels of parallel evolution.

Lastly, by preparing a cladogram for a given group of organisms based on non-ecological traits (i.e., structural rather than functional traits), then mapping ecological diversification onto the tree (Farris optimization: Farris, 1970), one can determine whether ecological diversification precedes or lags behind morphological diversification (see e.g., Ross, 1972a, 1972b; Resh et al., 1976; Morse & White, 1979). Such analyses can have startling effects. Brooks et al. (1985b) recently finished a family-level analysis of digenetic trematodes, based on 211 morphological characters. When all data for six different *categories* of ecological diversification were mapped onto the cladogram, only 26% of the tree was resolved. The historical picture is one of ecological diversification lagging behind morphological diversification. Ross (1972b) estimated that one ecological shift occurs for approximately 30 speciation events in phytophagous insects. Boucot (1983b) has suggested that this ecological conservatism is a general picture in the fossil record.

		Origin of Association	
		Coevolution	Colonization
ECOLOGICAL TRAIT	plesiomorphic	H - H	H - R
	autapomorphic	R - H	R - R

FIGURE 17. Two by two contingency table showing possible evolutionary explanations for observed ecological associates and individual ecological life history traits. H = historical, or inherited; R = recent, or modified in the given case.

The applications of historical ecological analysis in this third area are just beginning. I will now present a case study to illustrate the kinds of applications I envision for historical ecology.

We may establish the topology of interactions for a given ecological association by direct observation. I have tried to show that it is possible to establish robust hypotheses of the relative recency of association among the members. By using those two types of data, it is possible to estimate the extent to which contemporary interactions are responsible for ecological life history traits. Species may occur together because they evolved together, vicariantly, or because at least one dispersed from its area of origin. Ecological life history traits exhibited by two or more interacting species may be traits inherited unchanged from ancestors or they may be traits that evolved concomitantly with the contemporary association. Figure 17 summarizes the four possible combinations of circumstances this provides.

For members of a vicariant association whose ecological interactions result from plesiomorphic (ancestral) ecological life history traits, their interactions may be completely explained by reference to historically determined properties of the organisms, namely, their inherited traits and their geographical history. There may also be associations in which at least one member has dispersed from its area of origin but for which interactions still result from expression of ple-

siomorphic ecological life history traits. For such associations only the contemporary ability of one (or more) of the species involved to disperse need be added to the historically determined traits to explain the observed interactions. For neither of these two classes of observations may contemporary ecological interactions be logically involved to explain the traits exhibited by the species involved.

The other two classes of observations are characterized by ecological life history traits unique to (evolving concomitantly with) a given contemporary association. Those traits may have arisen independently of ancestral interactions or may have arisen as a result of ancestral interactions. Only for the latter case can it be said that influences extrinsic to the organism, in this case the ecological interactions of other species, were responsible in any way for a particular set of traits that we observe today.

In many cases, it is possible for different equally-parsimonious interpretations of the ancestral condition to be postulated (Farris, 1970; Mickovich, 1982; Swofford & Maddison, unpubl. data). The examples that I will present next have been chosen so that they are relatively unambiguous, but research into the properties and assumptions of various optimization schemes for predicting ancestral traits is of utmost importance for applying this technique generally.

Holmes (1973) reported that the digeneans *Psettarium Sebastodorum* and *Aporocotyle Macfarlani*, inhabiting the circulatory system of rockfishes, exhibited little niche overlap. *Psettarium Sebastodorum* occurs almost exclusively in the heart whereas *A. Macfarlani* is almost entirely restricted to the blood vessels of the gill arches. Holmes assumed that parasite community structure is affected to a large degree by interspecific competition. From this, he concluded that the non-interactive site selection by the two species of blood flukes was de facto evidence of past competition.

Rohde (1979) examined the same data as Holmes. He assumed that natural selection could explain the observed differences in site selection easily. All one need do is invoke the notion that selection would favor flukes that clumped together in the host because they would have a higher probability of mating. His conclusions: one need not invoke competition to explain the observations. The data are evidence of the effectiveness of natural selection.

Price (1977, 1980) also examined Holmes' data.

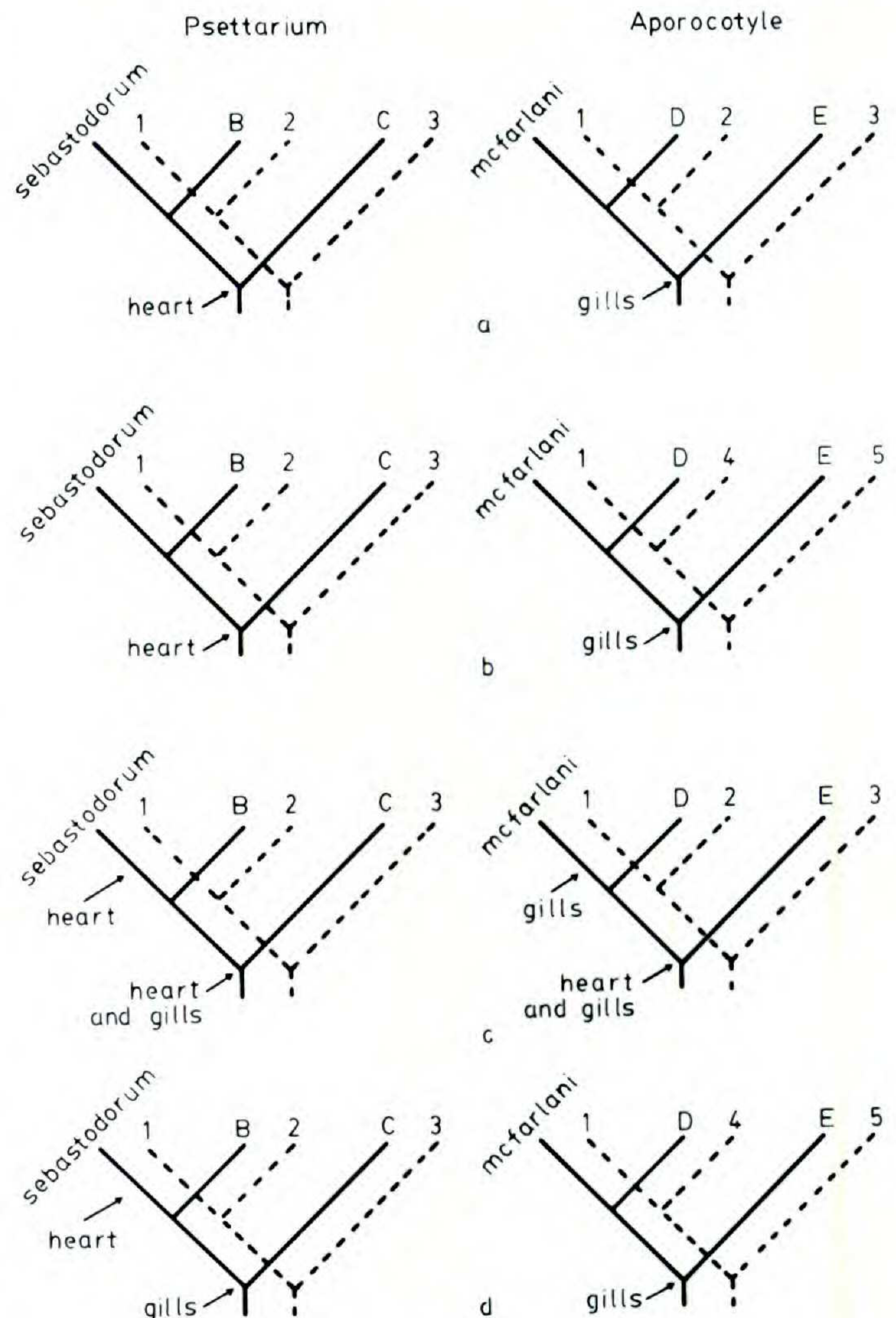


FIGURE 18. Predicted sets of cladograms for rockfish hosts and two groups of blood flukes, including the site selection traits for the flukes, under each of the four contingencies listed in Figure 17.—a. Historically determined association and traits.—b. Historically determined traits, recent (colonizing) association.—c. Historically determined association, recent (autapomorphic) traits.—d. Recent (colonizing) association and recent (autapomorphic) traits (redrawn from Brooks, 1980a).

His assumption was that parasite communities, because they are generally found to be below MacArthur-Wilson (MacArthur & Wilson, 1967) equilibrium, are never established and persistent for long periods but are always young colonizing communities. He further asserted that generalized parasites are young colonizers and specialized parasites are not. Given the two specialized parasites in a young colonizing community, Price concluded that the parasites were pre-adapted to their specialized niches and therefore colonized them. Competition and selection played minimal roles in their site selection in rockfish.

Finally, Brooks (1980a, 1980b) suggested that the parasites could be part of a coevolving fauna, that is, a vicariant ecological association, exhibiting plesiomorphic ecological life history traits

for site specificity (habitat loyalty). The four different opinions each correspond to one of the general classes listed in Figure 17 and are shown in Figure 18. Brooks (1980a, 1980b) suggested that each of the four explanations predicted an explicit set of phylogenetic relationships and shifts in characters and/or hosts.

For Brooks' contention to be correct, the two different parasites must exhibit a vicariant (= coevolving) relationship with the same host group and must exhibit plesiomorphic life history traits. Figure 18a summarizes those attributes. Price's hypothesis (Figure 18b) would not differ too greatly, except that either *Psettarium* or *Aporocotyle*, or both, would be colonizers in rockfish, so the host-parasite relationships indicated by each parasite group would differ. Rohde's hypothesis involves hosts and parasites that are together for a considerable period of time during which natural selection promotes progressively narrower site selection. This is shown in Figure 18c, where the parasites exhibit vicariant host relationships as well as autapomorphic ecological life history traits. Finally, we consider Holmes' hypothesis of competitive interactions mediating site selection (Fig. 18d). Corroboration of this class of hypotheses requires both elements of dispersal and the expression of autapomorphic traits relevant to the dispersal. Autapomorphic traits are features of the evolutionary context of the ecological interactions.

Holmes and Price (1980) attempted to analyze the *Psettarium*/*Aporocotyle*/rockfish system according to the above protocol. They concluded that there was no historically determined component in the interaction. Both species of parasites were deemed to be colonizers of rockfish and were "ecological specialists" in other hosts. Note that this corresponds to the situation found in Figure 18b, in which the ecological life-history traits exhibited are plesiomorphic, that is, historically constrained. Thus, Holmes and Price were incorrect in asserting that their conclusions supported strict ecological determinism. They also asserted that: "... the genealogies of parasites and their hosts are clearly not congruent (eliminating all four cases of Brooks' Figure 4)." Brooks' "Figure 4" refers to Figure 18. Note that for only Figure 18a and 18c are host and parasite genealogies congruent. Note also that Figure 18b corresponds to the conclusions Holmes and Price drew. Thus, they were also incorrect in saying that they had eliminated all four cases Brooks (1980a) proposed. These inconsistencies in their

conclusions led me to re-examine Holmes and Price's phylogenetic hypotheses. Regarding *Psettarium*, they wrote: "The genealogy of three species of *Psettarium* is not clear (see differentiating characteristics in Holmes, 1971). However, it does not appear that *P. japonicum* and *P. tropicum* are more closely related to each other than to *P. Sebastodorum*. The male terminal genitalia of *P. Sebastodorum* are more similar to those of *P. japonicum* than to those of *P. tropicum*, suggesting the genealogy of figure 2B." Upon examining the primary literature, I found that the similarity in male terminal genitalia between *P. Sebastodorum* and *P. japonicum* is based on their possession of a cirrus sac (a bag containing the male intromittent organ)—*P. tropicum* lacks a cirrus sac. However, the presence of a cirrus sac is plesiomorphic not just for fish blood flukes, but for all flukes. Therefore, its absence in *P. tropicum* is not indicative that *P. Sebastodorum* and *P. japonicum* are each other's closest relatives. However, *P. tropicum* and *P. japonicum* are both wide-bodied, whereas *P. Sebastodorum* is slender and elongate. In order to determine which trait might be plesiomorphic, we needed to examine close relatives (out-groups) of *Psettarium* spp. Manter (1954) had stated that the differences between *Psettarium* and the genus *Cardicola* were "not clear" and "seemed rather inadequate." Holmes (1971) stated: "These two genera [*Psettarium* and *Cardicola*] are very similar, and certainly do not belong to different subfamilies." Of the nine species of *Cardicola*, some are elongate and some have wide bodies. Finding no clearcut support within *Cardicola*, I then examined two other related species, namely, *Paracardicola hawaiiensis* and *Neoparacardicola nasonis*. Both of these species have two testes, the plesiomorphic condition for flukes. Members of *Cardicola* and *Psettarium* have only one testis; thus, they would seem to form a monophyletic group based on that trait. Both *P. hawaiiensis* and *N. nasonis* are elongate worms, suggesting that elongate bodies are plesiomorphic for the group. Thus, *Psettarium tropicum* and *P. japonicum* would be closest relatives based on sharing the apomorphic trait of wide bodies. *Psettarium* is supposed to be discrete from *Cardicola* by virtue of possessing a bend in the posterior margin of the body at the point of the male genital pore. However, *Neoparacardicola nasonis* exhibits that trait, making it either a convergent trait or a plesiomorphic trait among these flukes. Thus, *Psettarium* has no real support as a mono-

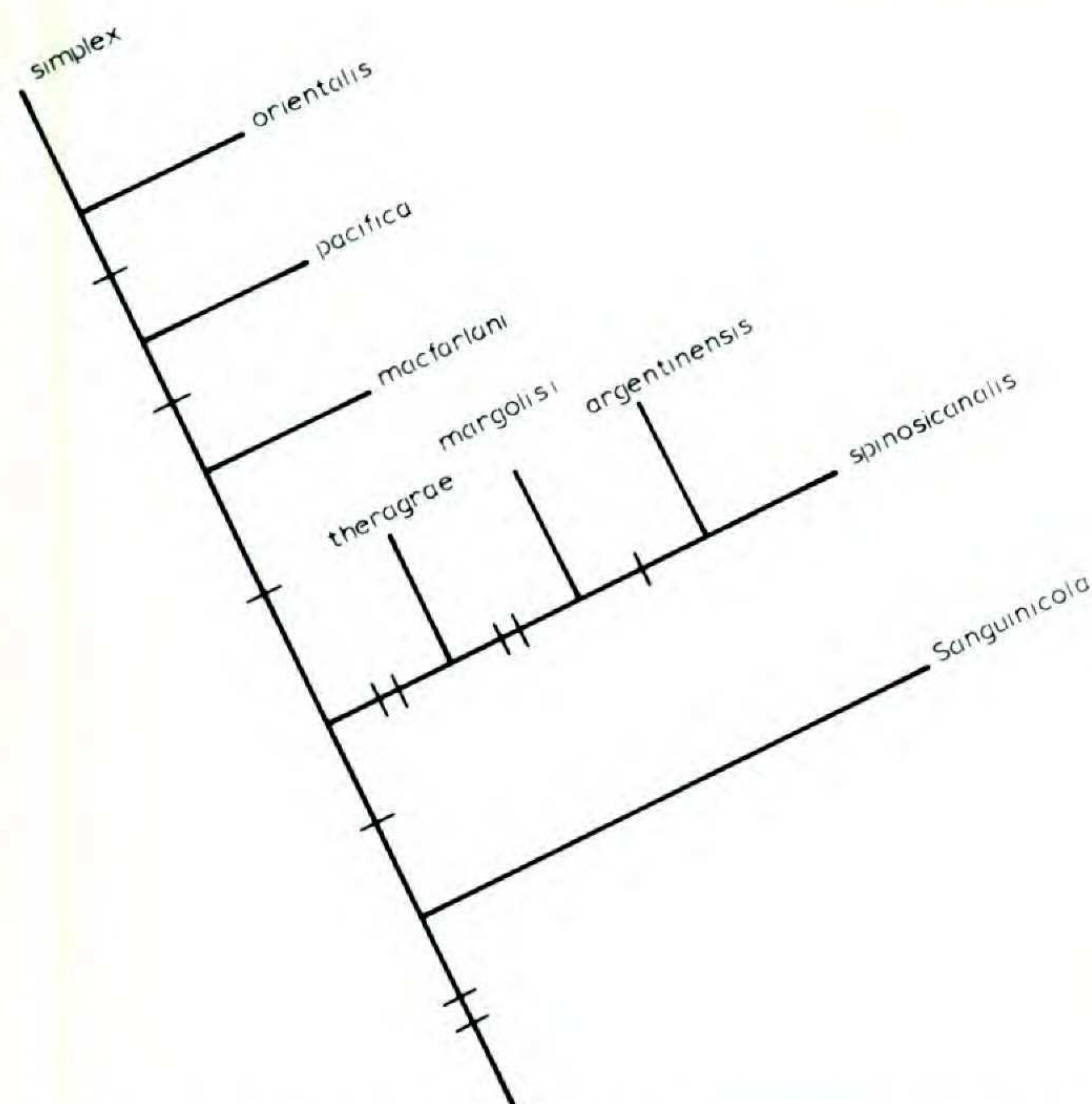


FIGURE 19. Cladogram depicting phylogenetic relationships of species of *Aporocotyle*, a genus of blood flukes inhabiting fish.

phyletic group distinct from *Cardicola*. *Cardicola*, however, has been distinguished only because it lacks the body bend of *Psettarium*; thus, there is no character support for *Cardicola* as a real group either. I will return to this point later.

The genealogy for *Aporocotyle* presented by Holmes and Price (1980) suffers from similar analytical flaws. Much of their cladogram is based on presence or absence and arrangement of body spines and number of testes. All members of *Aporocotyle* have multiple testes, as do members of their closest relative, *Sanguinicola*. However, as mentioned before, the plesiomorphic number of testes in flukes is two. Holmes and Price's genealogy of *Aporocotyle* arranges species beginning with those having more than 130 testes and terminating with those having 25–32 testes. Out-group comparisons would support a reversal of that trend. In addition, enlarged lateral body spines are used as indicators of relationships among species of *Aporocotyle*, even though *Sanguinicola* spp. have them as well. Figure 19 depicts the phylogenetic hypothesis best supported by those characters re-interpreted in strictly phylogenetic terms.

In Figure 20, the cladogram for *Aporocotyle* and one for the three *Psettarium* species are displayed, with their host groups superimposed in place of species names. Although there is not much resolution, there is no evidence supporting host-switching. The possible vicariant association between the two groups of blood flukes and

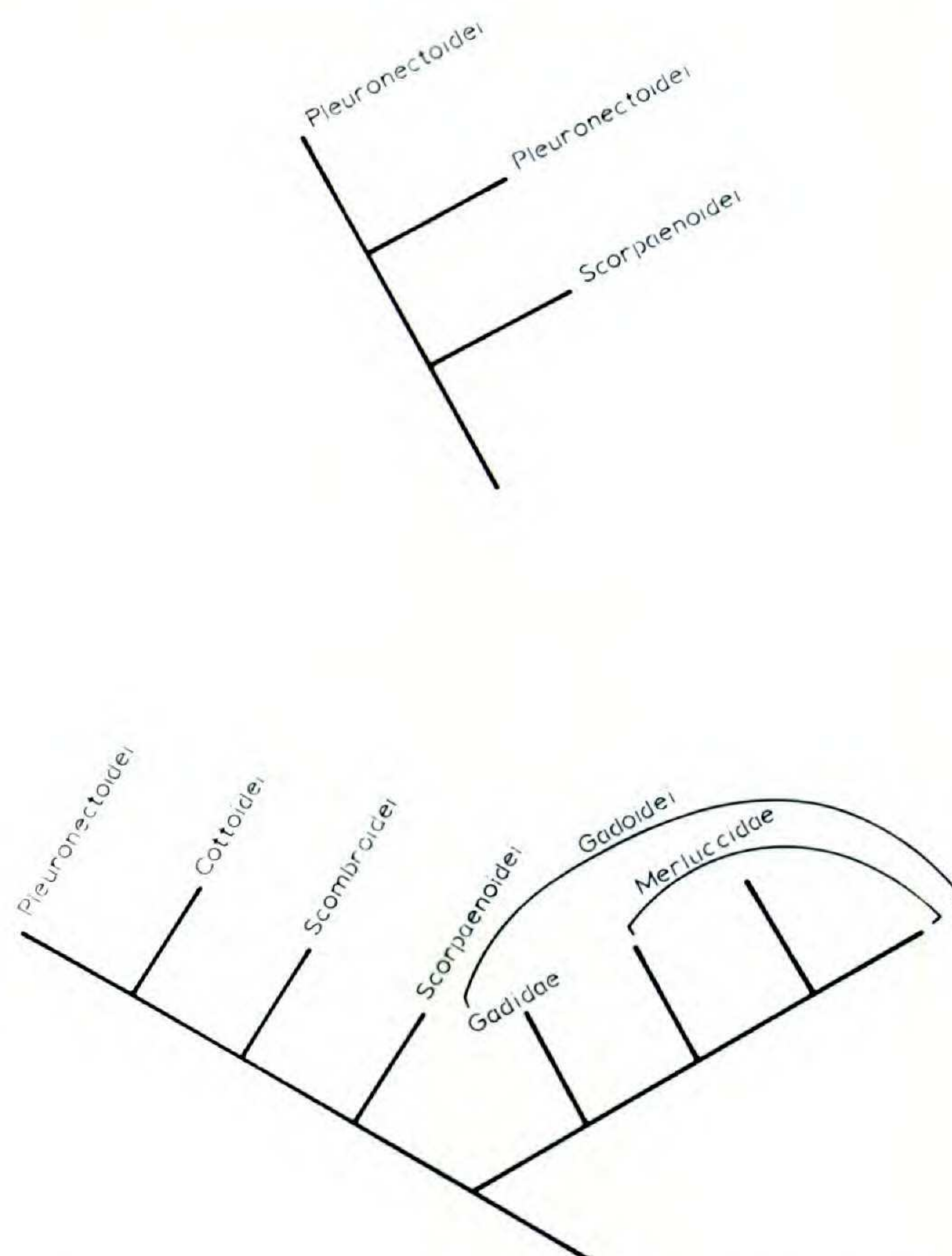


FIGURE 20. Host relationships indicated by phylogenetic relationships of *Psettarium* spp. (top) and *Aporocotyle* spp. (bottom).

the various host groups could be better examined if species of *Psettarium* occurred in cottoids or scombroids. Interestingly, four species of *Cardicola* occur in cottoids and three in scombroids. At least one of those occurring in cottoids, *C. laruei*, has a wide body like *P. japonicum* and *P. tropicum*. [The remaining two species of *Cardicola* inhabit mugiloid and labroid fishes, respectively.] Figure 21 shows Figure 20a redrawn to include the species of *Cardicola*; Figure 22 shows the relative relationships of the fish groups involved and their associated blood flukes.

The new analysis demonstrates no incongruence among the host and parasite cladograms (Fig. 23). However, the vast majority of species of fish in each of the host groups have no blood flukes reported from them. This suggests that (sampling error aside) although both groups of blood flukes have coevolved with their hosts, that coevolution has been marked by independent failure of the two groups of flukes to persist in all evolving host lineages. The absence of parasites from many hosts does not indicate the degree of relationship among those that survive. It is not inconsistent with coevolution that in only one known case do members of *Aporocotyle* and

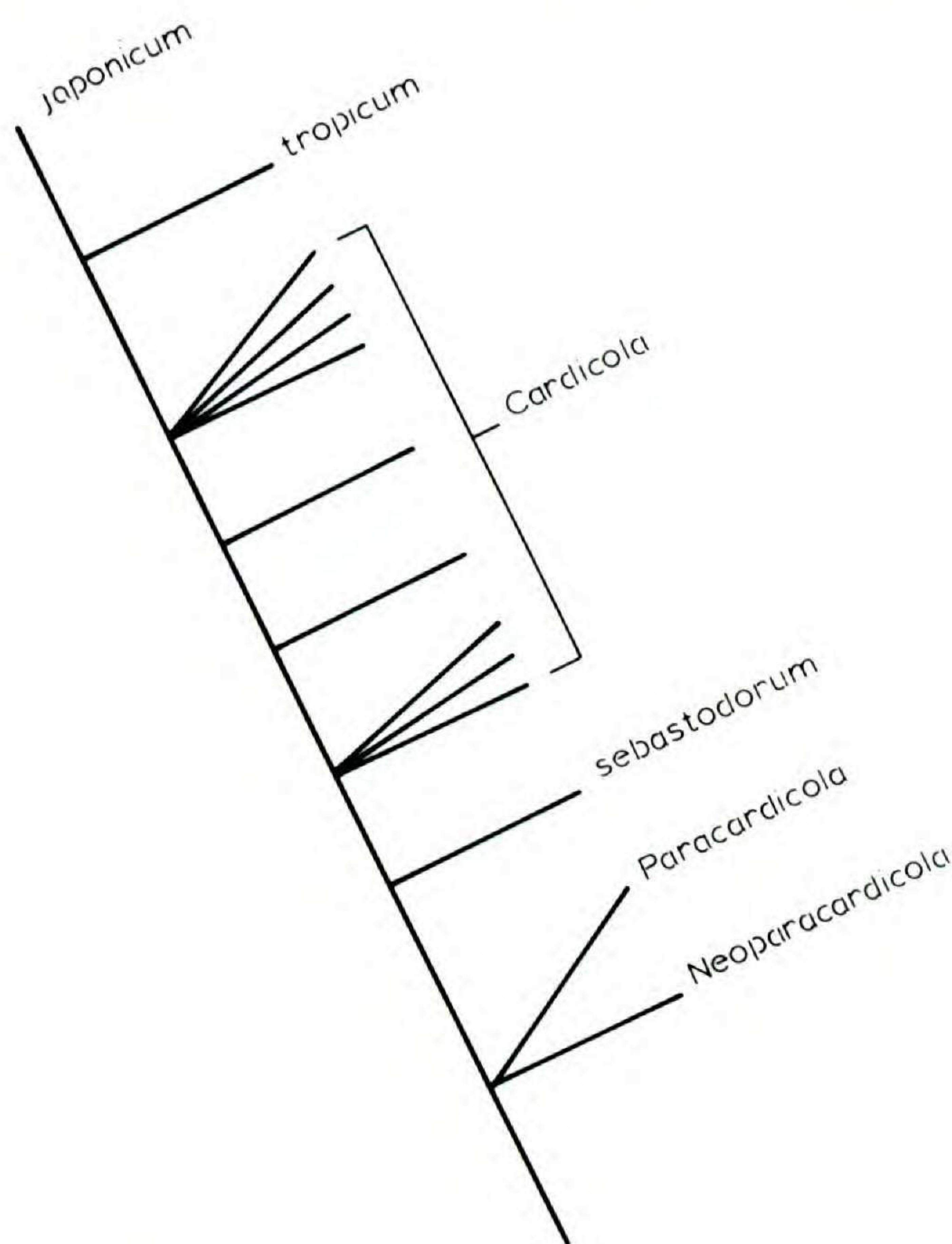


FIGURE 21. Phylogenetic relationships of *Psettarium* spp. (*P. japonicum*, *P. tropicum*, *P. sebastodorum*), *Cardicola* spp., and two outgroups (*Paracardicola* and *Neoparacardicola*). Note that *Psettarium* is polyphyletic and *Cardicola* is paraphyletic.

Psettarium-Cardicola occur in the same host. This is especially true if the hosts in which the co-occurrence happens are relatively primitive, as they are in this case.

Having established the temporal context of the association between *Aporocotyle macfarlani*, *Psettarium sebastodorum*, and *Sebastes* spp., we may now examine the possibility of interactive or non-interactive factors determining the site-selection exhibited by the parasites. For this we take the two parasite cladograms and superimpose their habitat site rather than the species names at the ends of the branches. We then estimate the ancestral conditions by means of “Farris optimization” (see Kluge & Farris, 1969; Farris, 1970) (Figs. 24, 25). Having those data, we may see that *A. macfarlani* occurs in the gills because its ancestor was a gill-inhabiting parasite but *P. sebastodorum* is most likely descended from a species that inhabited the mesenteric blood vessels. Thus, *P. sebastodorum* exhibits an autapomorphic trait for site selection. This would appear to support Rohde’s hypothesis, for that species at least. However, no other species in the group shows a similar tendency. The shift in traits

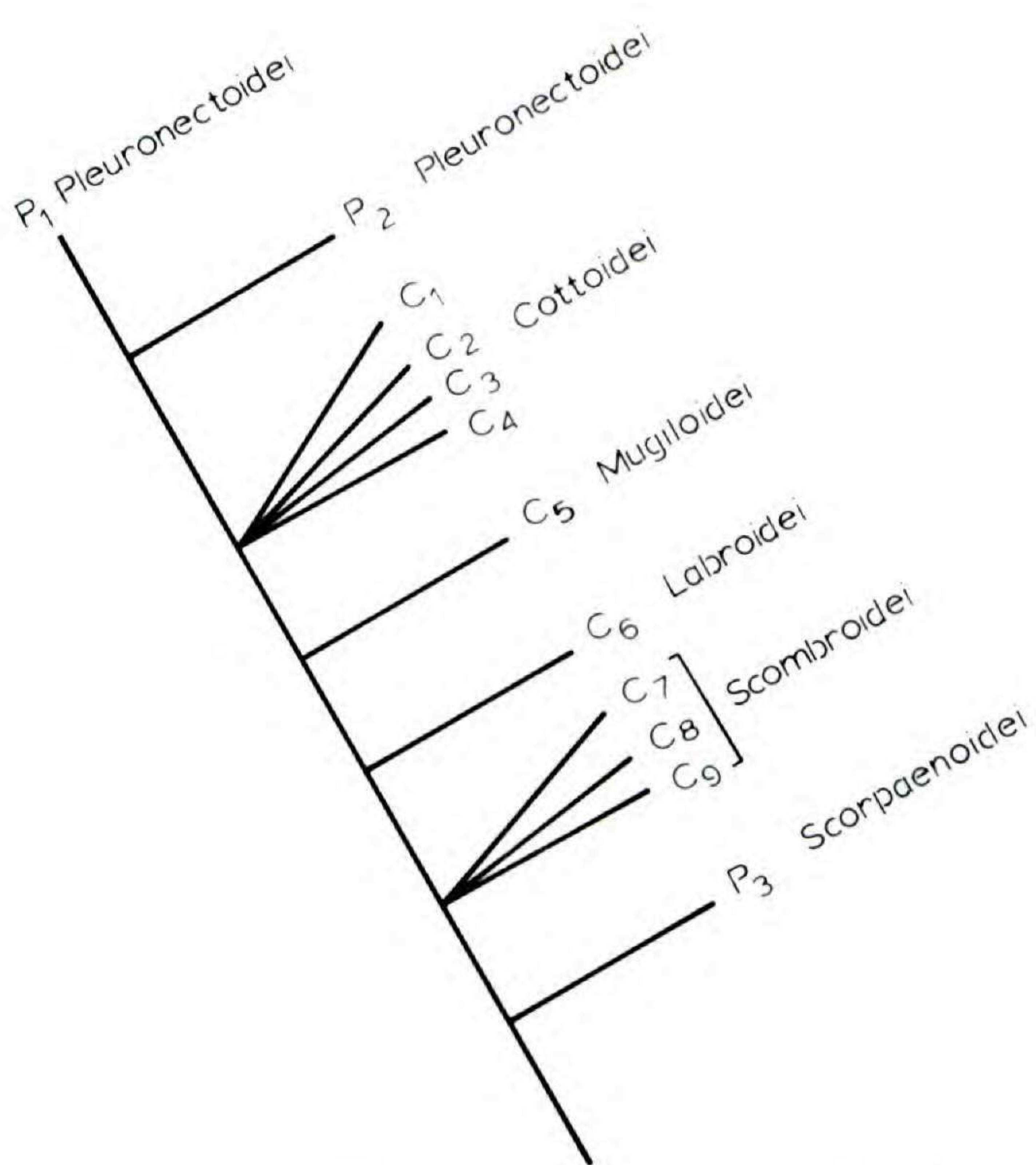


FIGURE 22. Host relationships indicated by phylogenetic relationships of *Psettarium/Cardicola* spp.

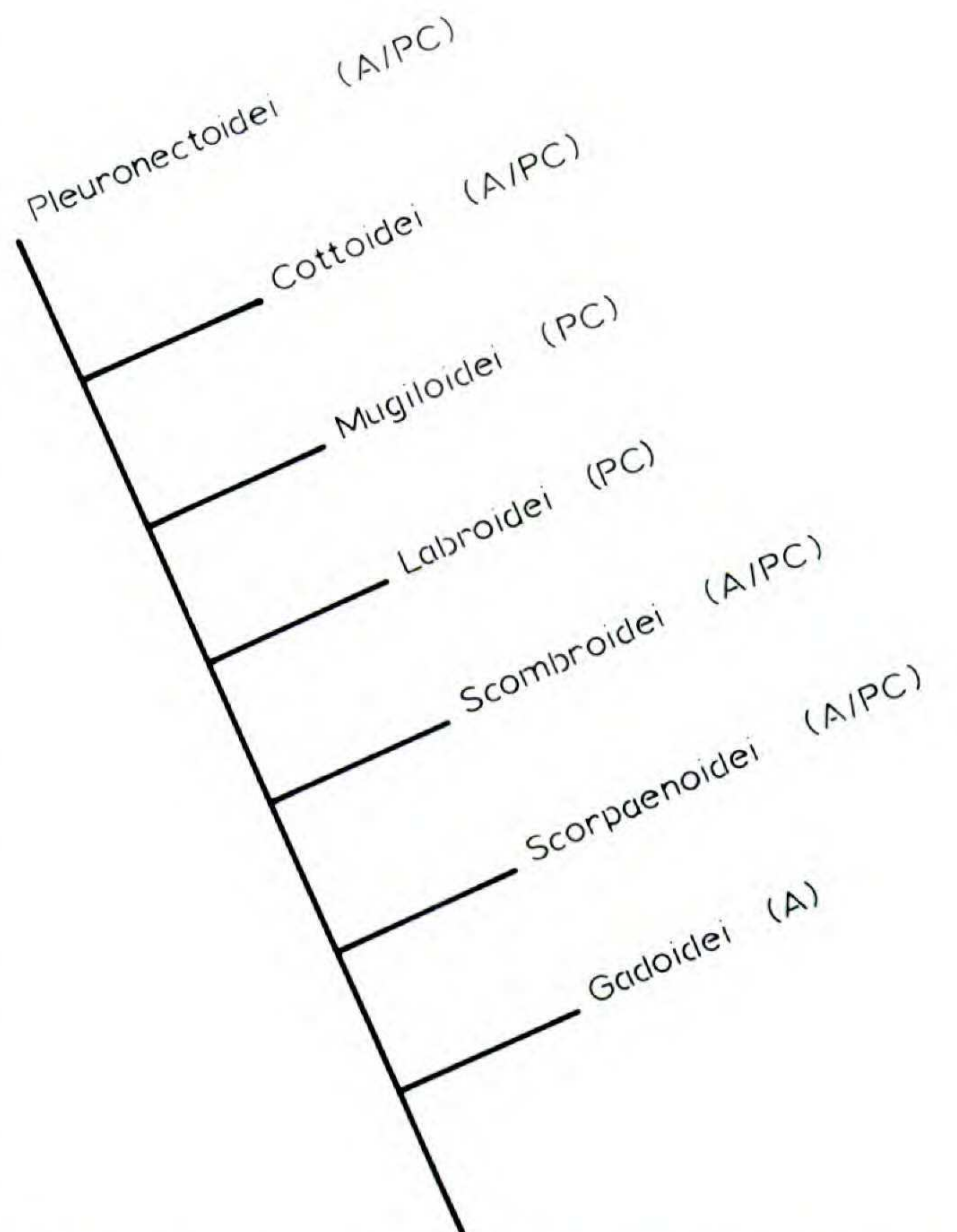


FIGURE 23. Summary set of host relationships supported by both *Aporocotyle* spp. (A) and *Psettarium/Cardicola* spp. (PC). Note congruence.

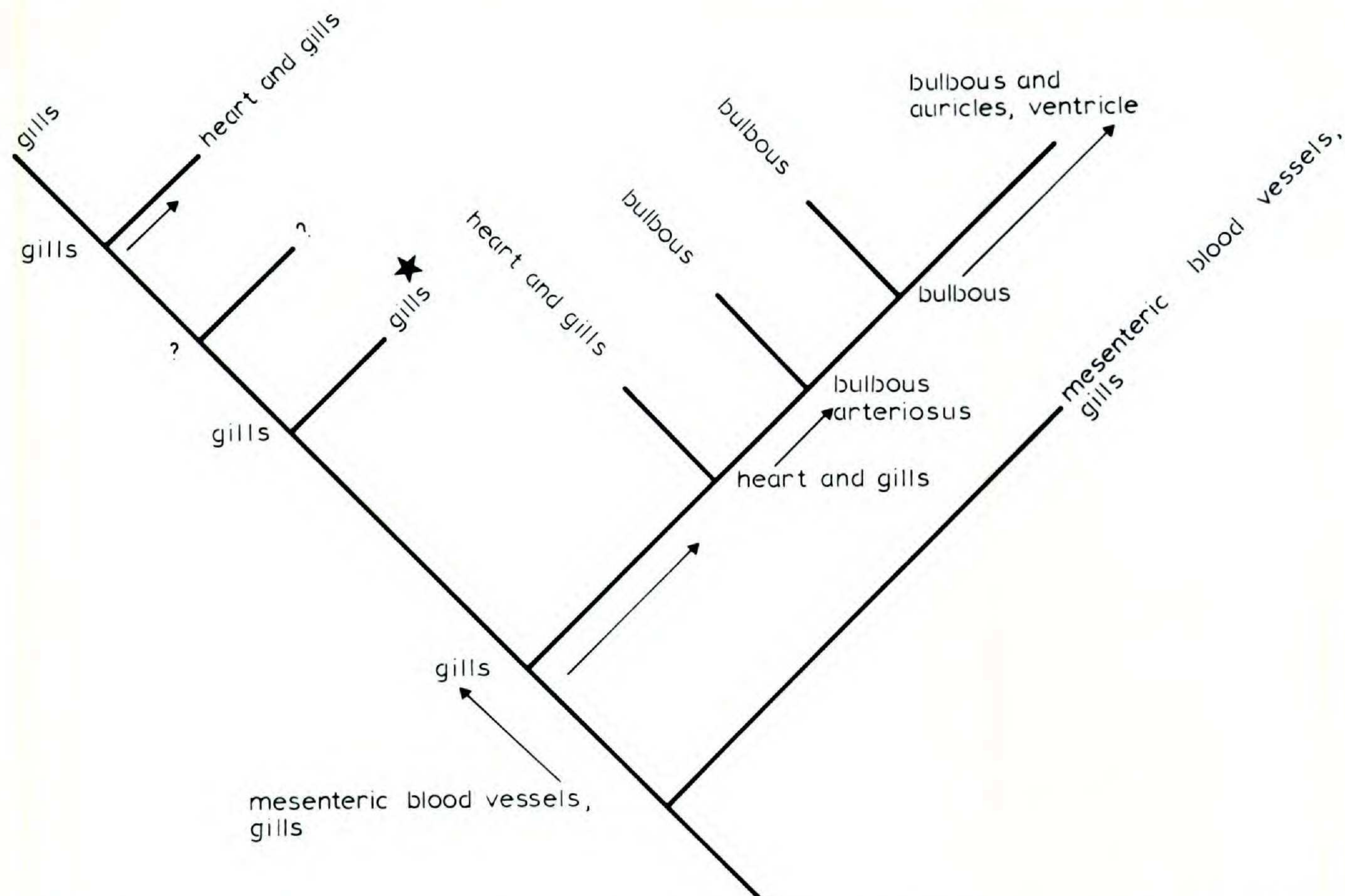


FIGURE 24. Summary of site selection traits for species of *Aporocotyle*. Arrows indicate required evolutionary changes; question mark indicates unknown data; star indicates *A. macfarlani*.

would not seem to be explicable in terms of competitive exclusion, because *A. macfarlani* does not occur in the mesenteric blood vessels. The change in site by *P. Sebastodorum* does not seem to be correlated with an extrinsic variable, so we conclude that the structure of this ecological association is historically determined. This contrasts with the South American freshwater sting-ray parasite associations that include some colonizers.

It is important to emphasize that historical evidence for adaptive changes of the type sought by evolutionary ecologists appear as exceptions to the historical pattern of structural and functional traits. Adaptive shifts are manifested by the same, or highly similar, traits arising in species that are not each other's closest relatives, but that share common ecological regime, in which the convergent traits are correlated with that particular ecological regime. In asking the question, "How often do such shifts occur?," Ross (1972b) concluded that for a survey of various insect groups the answer was 1–20%, with an average of about 3% (one in every 30 speciation events). This accords well with my studies of parasitic helminths. If this is generally true, there does not

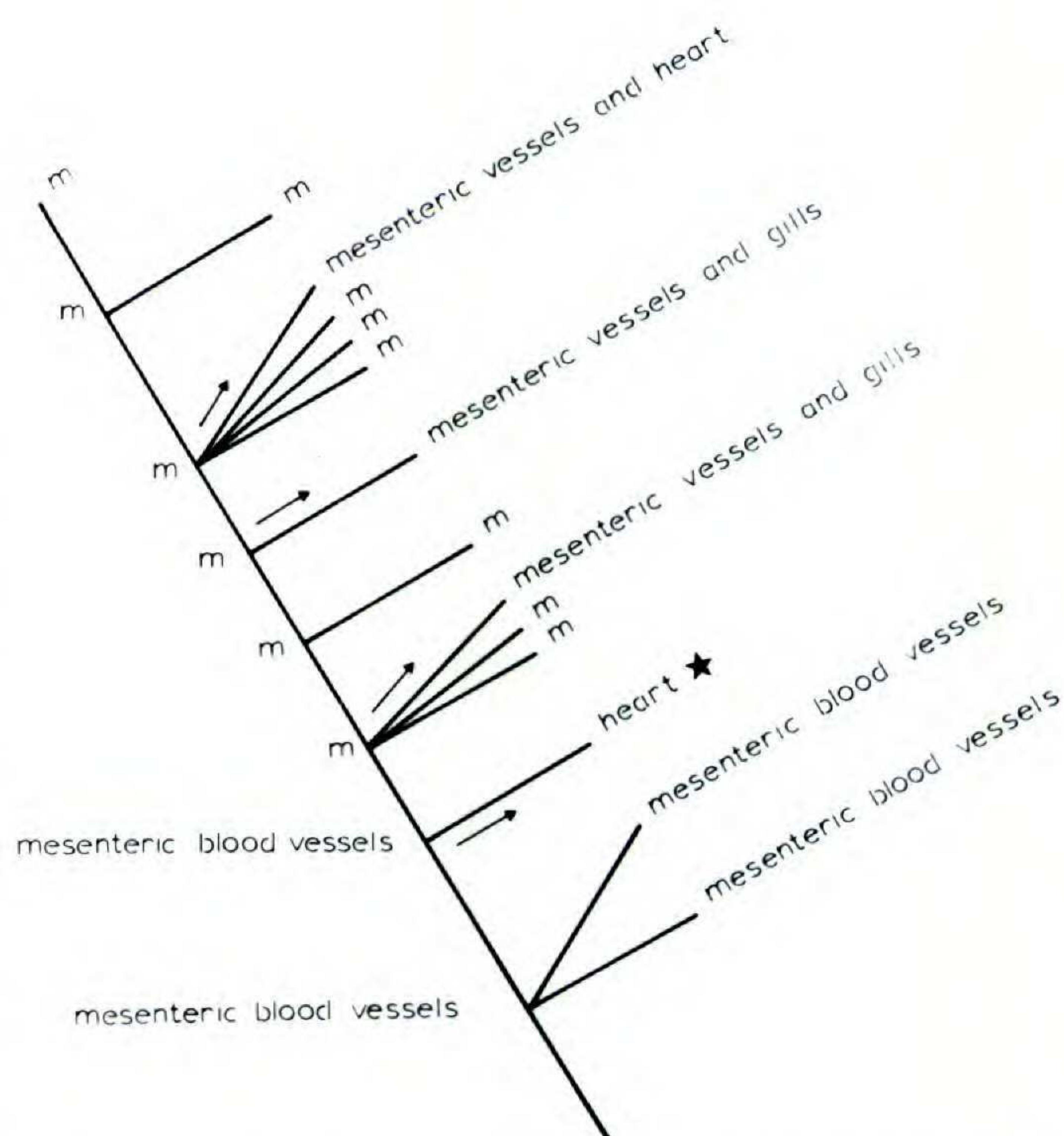


FIGURE 25. Summary of site selection traits for species of *Psettarium/Cardicola*. Arrows indicate required evolutionary changes; star indicates *P. sebastodorum*.

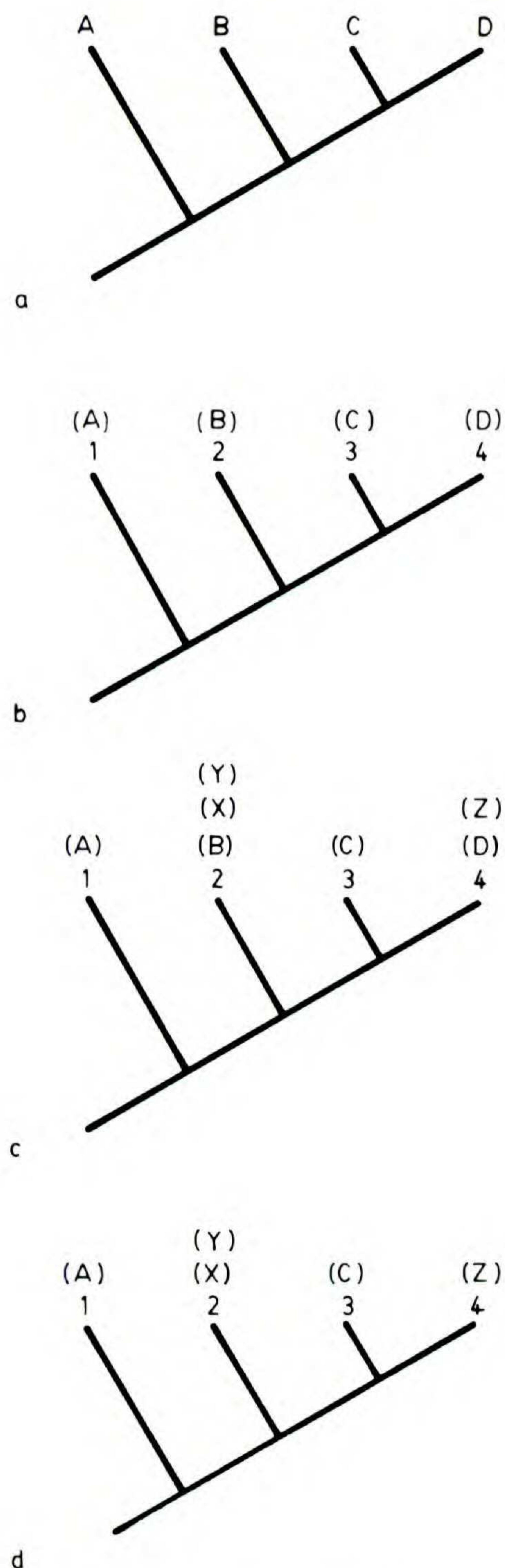


FIGURE 26. Demonstration that degree of co-accommodation (host specificity) need not be great in order for the method proposed in this study to detect historical patterns.—a. Depicts a host taxon's phylogenetic relationships.—b. Shows that the parasite taxon 1-2-3-4 has co-specified with the host taxon.—c. Depicts broadening co-accommodation by some members of the parasite taxon; note that co-speciation of ABCD and 1-2-3-4 can still be discerned.—d. Depicts the host-parasite relationships of parasite taxon 1-2-3-4 if B and D are no longer host members of the parasite taxon. In this case, even though a number of unrelated hosts are used, the historical pattern is still present (redrawn from Brooks, 1981b).

seem to have been enough ecological diversification to explain evolutionary diversification.

If historical constraints play a major role in determining ecological structure, we would ex-

pect to find evidence of them at higher systematic levels than the species. As mentioned before, Brooks et al. (1985b) recently presented a phylogenetic analysis of the 62 families of digeneans (to which *Psettarium*, *Cardicola* and *Aporocotyle* belong). Only 26% of the groupings and 35% of all branches on the phylogenetic tree were characterized by ecological changes. Classes of ecological traits considered were: (1) changes in developmental programs producing increased numbers of infective larvae, (2) changes in encystment behavior of infective larvae, (3) shifts in first host, (4) acquisition of and shifts in second hosts, (5) shifts in final host, and (6) changes in site of infection in the final host. Ecological changes definitely lagged behind morphological changes. Trends seen in species-level analyses are found in family-level analyses as well, attesting to the influence of historical constraints on ecological diversification.

SUMMARY

Historical ecology provides a missing component in studies of the evolution of ecological associations—history. This may seem like a strange assertion, since it is certainly true that evolutionary ecologists are vitally interested in historical phenomena. I think two perceptions have led to the exclusion of historical components in evolutionary ecology. The first is the perception that there exists no protocol for producing direct estimates of history that has any degree of empirical rigor. I hope that my few examples and the rest of the contributions in this volume provide reason for optimism that such a protocol is now firmly entrenched. The second perception goes something like this: even if we could provide direct estimates of history, the indirect measures we use now give us the same answers. Historical ecology allows us to investigate this perception.

In the past, I have examined three components of the evolutionary ecology of host-parasite systems: (1) "equilibrium" numbers of species, (2) host specificity, and (3) "resource-tracking" models (see Brooks, 1979b, 1980a, 1980b, 1981b). Consider the following possibilities derived from historical analysis. Suppose we discover an association that is very old and historically structured, such as the Parana River system stingray parasite fauna, and yet that association exists below predicted "equilibrium" numbers. Price (1980) noted that parasite communities

generally exist below equilibrium numbers and used that observation as evidence that parasite community structure reflects young, colonizing phenomena. From the historical perspective, it seems that the notion of "equilibrium" numbers of species may be an artifact of one theory of community evolution rather than empirical necessity.

Now let us consider the question of host specificity from the historical perspective. I have suggested previously that degree of host specificity is decoupled from historical association of lineages. Figure 26 provides an example of this. Notice that no matter what differences exist in degree of host specificity, the history of the parasite lineage is still coordinate with that of the original host lineage. Conversely, it is not necessarily true that very pronounced (host) specificity indicates a long-standing association. Finally, a related concept is that of "resource tracking" models of coevolution (see e.g., Kethley & Johnston, 1975). Resource-tracking models imply a set of specific historical predictions that are seldom, if ever, acknowledged. Chief among these is the assertion that not only do ancestors always persist, ancestors are always among the known species at any given time (see Brooks, 1981b for a fuller discussion). Thus, it seems that it is not true that the indirect estimates of history will always provide the same answers as explanations derived from direct estimates of history. Hence my assertion, at the beginning of this review, that historical ecology provides a complementary approach with evolutionary ecology to attaining insights into causal mechanisms of the evolution of ecological associations. Certainly the most interesting questions will involve cases in which the two approaches give different answers.

Finally, I would like to comment on the view, from historical ecology, of the current enthusiastic exchanges among ecologists concerning the relative merits of "competition" or "random association" null hypotheses in explaining the structure, or organization, of communities (see Lewin, 1983a, 1983b for a review). To do so, we must first represent the question in historical terms, then produce maximum randomness and minimum randomness configurations. I tried to show how to represent such questions in historical terms using the fish blood fluke example. A convenient measure of the relative randomness of an association of species and their ecological life history traits is the statistical entropy of the community ensemble. Using the method pi-

oneered by Karreman (1955) and modified for use in examining phylogenetic questions (Wiley & Brooks, 1983), it is possible to show that the minimum randomness configuration is the one that is wholly determined historically. It is also possible to show that maximum randomness is not achieved by a random assemblage of species with fixed traits, but by the assemblage (random or not) of species with unlimited polymorphism for ecological traits; in other words the maximum randomness null hypothesis is indistinguishable from a maximum competition model when viewed historically. Somewhere in between lie all systems experiencing some competitive interactions. All of these are relatively more random than historically determined ecological associations. Thus, from the perspective of historical ecology, it is difficult to understand the hypothesis that competition is an organizing force in evolution. Accounting for such differences in perspective should provide exciting research projects in the future.

LITERATURE CITED

- ANDREWS, J. M. 1927. Host-parasite specificity in the coccidia of mammals. *J. Parasitol.* 13: 183-194.
- ASHLOCK, P. D. 1974. The uses of cladistics. *Annual Rev. Ecol. Syst.* 5: 81-99.
- BAER, J.-G. 1948. Les helminthes, parasites des vertebres. Relations phylogenetique entre leur evolution et celle de leurs hotes. *Ann. Sci. Franche-Comté* 2: 99-113.
- BOUCOT, A. J. 1983a. Area-dependent-richness hypotheses and rates of parasite/pest evolution. *Amer. Naturalist* 121: 294-300.
- . 1983b. Does evolution take place in an evolutionary vacuum? *J. Paleontol.* 57: 1-30.
- BOWLER, P. J. 1983. *The Eclipse of Darwinism*. Johns Hopkins Univ. Press, Baltimore.
- BROOKS, D. R. 1979a. Testing hypotheses of evolutionary relationships among parasites: the digeneans of crocodilians. *Amer. Zool.* 19: 1225-1238.
- . 1979b. Testing the context and extent of host-parasite coevolution. *Syst. Zool.* 28: 299-307.
- . 1980a. Allopatric speciation and non-interactive parasite community structure. *Syst. Zool.* 29: 192-203.
- . 1980b. Brooks' response to Holmes and Price. *Syst. Zool.* 29: 214-215.
- . 1981a. Revision of the Acanthostominae (Digenea, Cryptogonimidae). *Zool. J. Linn. Soc.* 70: 313-382.
- . 1981b. Hennig's parasitological method: a proposed solution. *Syst. Zool.* 30: 229-249.
- & D. R. GLEN. 1982. Pinworms and primates: a case study in coevolution. *Proc. Helminthol. Soc. Wash.* 49: 76-85.
- & C. MITTER. 1984. Analytical aspects of coevolution. Pp. 42-53 in Q. D. Wheeler & S. Black-

- well (editors), *Insect-Fungus Relationships. Perspectives in Evolution and Ecology*. Columbia Univ. Press, New York.
- , R. T. O'GRADY & D. R. GLEN. 1985a. The phylogeny of the *Cercomeria* Brooks, 1982 (Platyhelminthes). *Proc. Helminthol. Soc. Wash.* 52: 1–20.
- , ——— & ———. 1985b. Phylogenetic analysis of the Digenea (Platyhelminthes: Cercomeria) with comments on their adaptive radiation. *Canad. J. Zool.* 63: 411–443.
- , M. A. MAYES & T. B. THORSON. 1981a. Systematic review of cestodes infecting freshwater stingrays (Chondrichthyes: Potamotrygonidae) including four new species from Venezuela. *Proc. Helminthol. Soc. Wash.* 48: 43–64.
- , T. B. THORSON & M. A. MAYES. 1981b. Freshwater stingrays (Potamotrygonidae) and their helminth parasites; testing hypotheses of evolution and coevolution. Pp. 147–175 in V. A. Funk & D. R. Brooks (editors), *Advances in Cladistics I*. New York Botanical Garden, New York.
- BRUES, C. T. 1920. The selection of food-plants by insects, with special reference to lepidopterous larvae. *Amer. Naturalist* 54: 313–332.
- CAIN, S. A. 1944. *Foundations of Plant Biogeography*. Harper and Row, New York.
- CAMERON, T. W. M. 1964. Host specificity and evolution of helminthic parasites. In B. Dawes (editor), *Advances in Parasitology*. Volume 9. Academic Press, London.
- CAMP, W. H. 1947. Distributional patterns in modern plants and the problems of ancient dispersals. *Ecol. Monogr.* 17: 159–183.
- CROIZAT, L., G. NELSON & D. E. ROSEN. 1974. Centers of origin and related concepts. *Syst. Zool.* 3: 265–287.
- DARLING, S. J. 1921. The distribution of hookworms in the zoological regions. *Science* 53: 323–324.
- DOGIEL, V. A. 1964. *General Parasitology*. Oliver and Boyd, London.
- DOUGHERTY, E. C. 1949. The phylogeny of the nematode family Metastrongylidae Leiper (1909): a correlation of host and symbiote evolution. *Parasitology* 39: 222–234.
- DUNN, E. R. 1925. The host-parasite method and the distribution of frogs. *Amer. Naturalist* 59: 370–375.
- EHRlich, P. R. & P. H. RAVEN. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18: 586–608.
- EICHLER, W. 1941a. Wirtsspezifität und stammesgeschichtliche Gleichlaufigkeit (Fahrenholz Regel) bei Parasiten in allgemeinen und bei Mallophagen im besonderen. *Zool. Anz.* 132: 254–292.
- . 1941b. Korrelation in der Stammesentwicklung von Wirten und Parasiten. *Z. Parasitenk.* (Berlin) 12: 94.
- . 1948. Some rules in ectoparasitism. *Ann. Mag. Nat. Hist.* 12: 588–598.
- EWING, H. E. 1924. On the taxonomy, biology and distribution of the biting lice of the family Gyropidae. *Proc. U.S. Natl. Mus.* 63: 1–42.
- . 1926. A revision of the American lice of the genus *Pediculus*, together with a consideration of the significance of their geographical and host distribution. *Proc. U.S. Natl. Mus.* 68: 1–38.
- FAHRENHOLZ, H. 1913. Ectoparasiten und abstammungslehre. *Zool. Anz.* (Leipzig) 41: 371–374.
- FARRIS, J. S. 1970. Methods for computing Wagner trees. *Syst. Zool.* 19: 83–92.
- HARRISON, L. 1911. The taxonomic value of certain parasites. *Annual Rep. Sydney Univ. Sci. Soc.* 1911–1912.
- . 1914. The Mallophaga as a possible clue to bird phylogeny. *Austral. Zool.* 1: 7–11.
- . 1915a. Mallophaga from *Apteryx*, and their significance: with a note on *Rallicola*. *Parasitology* 8: 88–100.
- . 1915b. The relationship of the phylogeny of the parasite to that of the host. *Rep. Brit. Assoc. Advancem. Sci.* 85: 476–477.
- . 1916. Bird-parasites and bird-phylogeny. *Ibis* 10: 254–263.
- . 1922. On the Mallophagan family Trimenoponidae, with a description of a new genus and species from an Australian marsupial. *Austral. Zool.* 2: 154–159.
- . 1924. The migration route of the Australian marsupial fauna. *Austral. Zool.* 3.
- . 1926. Crucial evidence for antarctic radiation. *Amer. Naturalist* 60: 374–383.
- . 1928a. On the genus *Stratiodrilus* (Archianelida: Histriobdellidae), with a description of a new species from Madagascar. *Rec. Austral. Mus.* 16: 116–121.
- . 1928b. Host and parasite. *Proc. Linn. Soc. New South Wales* 53: ix–xxxi.
- . 1929. The composition and origins of the Australian fauna, with special reference to the Wegner hypothesis. *Rep. Meetings Australas. Assoc. Advancem. Sci.*
- HEGNER, R. W. 1928. The evolutionary significance of the protozoan parasites of monkeys and man. *Quart. Rev. Biol.* 3: 225–244.
- HENNIG, W. 1966. *Phylogenetic Systematics*. Univ. Illinois Press, Urbana.
- HOLMES, J. C. 1971. Two new sanguinicolid blood flukes (Digenea) from scorpaenid rockfishes (Perciformes) of the Pacific coast of North America. *J. Parasitol.* 57: 209–216.
- . 1973. Site selection by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. *Canad. J. Zool.* 51: 333–347.
- & P. W. PRICE. 1980. Parasite communities: the roles of phylogeny and ecology. *Syst. Zool.* 29: 203–213.
- HOPKINS, G. H. E. 1942. The Mallophaga as an aid to the classification of birds. *Ibis* 6: 94–106.
- IHERING, H. VON. 1891. On the ancient relations between New Zealand and South America. *Trans. & Proc. New Zealand Inst.* 24: 431–445.
- . 1902. Die Helminthen als Hilfsmittel der zoogeographischen Forschung. *Zool. Anz.* (Leipzig) 26: 42–51.
- INGLIS, W. G. 1971. Speciation in parasitic nematodes. Pp. 185–223 in B. Dawes (editor), *Advances in Parasitology*. Volume 9. Academic Press, London.
- JOHNSTON, S. J. 1912. On some trematode parasites

- of Australian frogs. *Proc. Linn. Soc. New South Wales* 37: 285–362.
- . 1914. Australian trematodes and cestodes. *Med. J. Australia* 1: 243–244.
- . 1916. On the trematodes of Australian birds. *J. & Proc. Royal Soc. New South Wales* 50: 187–261.
- KARREMAN, G. 1955. Topological information content and chemical reactions. *Bull. Math. Biophys.* 17: 279–285.
- KELLOGG, V. L. 1896. New Mallophaga, I. With special reference to a collection made from maritime birds of the Bay of Monterey, California. *Proc. Calif. Acad. Sci.* 6: 31–168.
- . 1913. Distribution and species-forming of ectoparasites. *Amer. Naturalist* 47: 129–158.
- & S. I. KUWANA. 1902. Mallophaga from birds. *Proc. Wash. Acad. Sci.* 4: 457–499.
- KETHLEY, J. B. & D. E. JOHNSTON. 1975. Resource tracking patterns in bird and mammal ectoparasites. *Misc. Publ. Entomol. Soc. Amer.* 9: 231–236.
- KIRBY, J., JR. 1937. Host-parasite relations in the distribution of protozoa in termites. *Univ. Calif. Publ. Zool.* 41: 189–212.
- KLUGE, A. G. & J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18: 1–32.
- LEWIN, R. 1983a. Santa Rosalia was a goat. *Science* 221: 636–639.
- . 1983b. Predators and hurricanes change ecology. *Science* 221: 737–740.
- MACARTHUR, R. H. & E. O. WILSON. 1967. *The Theory of Island Biogeography*. Princeton Univ. Press, Princeton, New Jersey.
- MANTER, H. W. 1940. The geographic distribution of digenetic trematodes of fishes of the tropical American Pacific. *Allan Hancock Pacific Exped.* 2: 531–547.
- . 1954. Some digenetic trematodes from fishes of New Zealand. *Trans. Roy. Soc. New Zealand* 82: 475–568.
- . 1955. The zoogeography of trematodes of marine fishes. *Exp. Parasitol.* 4: 62–86.
- . 1963. The zoogeographical affinities of trematodes of South American freshwater fishes. *Syst. Zool.* 12: 45–70.
- . 1966. Parasites of fishes as biological indicators of recent and ancient conditions. Pp. 59–71 in J. E. McCauley (editor), *Host-Parasite Relationships*. Oregon State Univ. Press, Corvallis.
- METCALF, M. M. 1920. Upon an important method of studying problems of relationship and geographical distribution. *Proc. Natl. Acad. U.S.A.* 6: 432–433.
- . 1922. The host parasite method of investigation and some problems to which it gives approach. *Anat. Rec.* 23: 117.
- . 1923a. The opalinid ciliate infusorians. *Bull. U.S. Natl. Mus.* 120: 1–484.
- . 1923b. The origin and distribution of the Anura. *Amer. Naturalist* 57: 385–411.
- . 1929. Parasites and the aid they give in problems of taxonomy, geographic distribution, and paleogeography. *Smithsonian Misc. Collect.* 81: 1–36.
- . 1940. Further studies on the opalinid ciliate infusorians and their hosts. *Proc. U.S. Natl. Mus.* 87: 465–634.
- MICHENER, C. D. 1967. Diverse approaches to systematics. Pp. 1–38 in T. Dobzhansky, M. K. Hecht & W. C. Steere (editors), *Evolutionary Biology*. Volume 4. Appleton-Century-Crofts, New York.
- MICKEVICH, M. F. 1981. Quantitative phylogenetic biogeography. Pp. 209–222 in V. A. Funk & D. R. Brooks (editors), *Advances in Cladistics I*. New York Botanical Garden, New York.
- . 1982. Transformation series analysis. *Syst. Zool.* 31: 461–478.
- MITTER, C. & D. R. BROOKS. 1983. Phylogenetic aspects of coevolution. Pp. 65–98 in D. J. Futuyma & M. Slatkin (editors), *Coevolution*. Sinauer Assoc., New York.
- MORSE, J. C. & D. F. WHITE, JR. 1979. A technique for analysis of biogeography and other characters in comparative biology. *Syst. Zool.* 28: 356–365.
- NELSON, G. & N. I. PLATNICK. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia Univ. Press, New York.
- PLATNICK, N. I. & G. NELSON. 1978. A method of analysis for historical biogeography. *Syst. Zool.* 27: 1–16.
- PRICE, P. W. 1977. General concepts on the evolutionary biology of parasites. *Evolution* 31: 405–420.
- . 1980. *Evolutionary Biology of Parasites*. Princeton Univ. Press, Princeton, New Jersey.
- PRITCHARD, M. H. 1966. Studies on digenetic trematodes of Hawaiian fishes: family Opecoelidae Ozaki, 1925. *Zool. Jahrb.* 93: 173–202.
- RESH, V. H., J. C. MORSE & I. D. WALLACE. 1976. The evolution of the sponge-feeding habit in the caddisfly genus *Ceraclea* (Trichoptera: Heptoceridae). *Ann. Entomol. Soc. Amer.* 69: 937–941.
- ROHDE, K. 1979. A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. *Amer. Naturalist* 114: 648–671.
- ROSEN, D. E. 1975. A vicariance model of Caribbean biogeography. *Syst. Zool.* 24: 431–464.
- . 1985. Geological hierarchies and biogeographic congruence in the Caribbean. *Ann. Missouri Bot. Gard.* 72: 636–659.
- ROSS, H. H. 1972a. An uncertainty principle in ecological evolution. In R. T. Allen & F. C. James (editors), *A Symposium on Ecosystematics*. Occas. Pap. Univ. Arkansas Mus. 4: 133–161.
- . 1972b. The origin of species diversity in ecological communities. *Taxon* 21: 253–259.
- STAMMER, H. J. 1957. Gedanken zu den parasitophyletischen Regeln und zur Evolution der Parasiten. *Zool. Anz.* 159: 255–267.
- SZIDAT, L. 1956. Der marine charakter der Parasitenfauna der Susswasserfische des Stromssystems des Rio de la Plata und ihre Deutung als Reliktfauna des Tertiärs Tethys-Meer. *Proc. XIV Int. Congr. Zool.* 1953: 128–138.
- . 1960. La parasitologia como ciencia auxiliar para develar problemas hidrobiologicos, zoogeograficos y geofisicos del Atlantico Sud. *Libro Homenaje Eduardo Cabellero*.
- VERSCHAFFELT, E. 1910. The cause determining the

- selection of food in some herbivorous insects. *Proc. Acad. Sci. Amsterdam* 13: 536–542.
- WILEY, E. O. & D. R. BROOKS. 1983. Nonequilibrium thermodynamics and evolution: a response to Løvtrup. *Syst. Zool.* 32: 209–219.
- WULFF, E. V. 1950. An Introduction to Historical Plant Biogeography. *Chronica Botanica Co.*, Waltham, Massachusetts. [Translation of 1932 Russian text.]
- ZSCHOKKE, F. 1933. Die Parasiten als Zeugen für die geologische Vergangenheit Ihrer Träger. *Forsch. & Fortschr.* 9: 466–467.